UNIVERSIDADE FEDERAL DO PARANÁ

VINICIUS MARCILIO DA SILVA

FLORESTA ATLÂNTICA: DISTRIBUIÇÃO DA DIVERSIDADE VEGETAL EM UM CONTEXTO ECONÔMICO E CONSERVACIONISTA

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VINICIUS MARCILIO DA SILVA

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Tese apresentada como requisito à obtenção do grau de Doutor em Ecologia e Conservação, no Curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, da Universidade Federal do Paraná.
Orientadora: Prof.ª Dr.ª Márcia C.M. Marques

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Curitiba, 21 de Fevereiro de 2017.

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“Los pájaros nacidos en una jaula,
piensan que volar es una enfermedad"
Alejandro Jodorowsky

RESUMO

O bioma Floresta Atlântica, um *hotspot* de biodiversidade, abriga a maior parte das terras cultivadas e da população do Brasil. Encontrar um caminho sustentável para o uso da terra nesse bioma é necessário, dado que as condições regionais e globais do clima, a provisão de comida e energia e a conservação da biodiversidade, estão todos em jogo. Aplicações da teoria ecológica podem auxiliar nesse objetivo de se atingir o desenvolvimento sustentável, conciliando produção e conservação da Floresta Atlântica. Essa tese teve como objetivo geral verificar o padrão de distribuição espacial da diversidade de espécies lenhosas em remanescentes da Floresta Atlântica e relacionar com indicadores de produção agrícola, a fim de subsidiar ações eficazes de conservação da biodiversidade neste bioma. A tese foi organizada em três capítulos tratando destes temas relacionados. O primeiro capítulo explorou os elementos da estrutura de metacomunidade e da diversidade da Floresta Atlântica e seus determinantes em diferentes escalas espaciais, com intuito de subsidiar políticas de conservação. A metacomunidade da Floresta Atlântica como um todo, bem como de seus tipos florestais (Florestas Ombrófila Densa, Ombrófila Mista e Estacional) apresentam estrutura de *nested subsets*, que representa subconjuntos aninhados com perda agrupada de espécies. Além disso, os componentes locais e geográficos da diversidade são responsáveis pela alta diversidade do bioma. Estes resultados demonstram que a diversidade da Floresta Atlântica é espacialmente estruturada e sugere que os esforços de conservação seriam mais efetivos focando na proteção de sítios ricos em diversidade. No segundo capítulo foi apresentado um breve histórico da agricultura na Floresta Atlântica a fim de se evidenciarem as grandes mudanças temporais das práticas agrícolas adotadas. As práticas de exploração econômica da Floresta Atlântica avançaram muito ao longo dos anos; iniciaram-se com um modelo extrativista, chegando à mecanização e diversificação de culturas. A quebra de paradigma do modelo agrícola foi um dos responsáveis por esses grandes avanços da agricultura no Brasil. Considerando as atuais ameaças à biodiversidade, sugere-se que o momento atual seja prenúncio de um novo paradigma na agricultura, onde o desenvolvimento agrícola seja baseado na sustentabilidade. O terceiro capítulo explorou *trade-offs* entre biodiversidade e produção agrícola na Floresta Atlântica, utilizando método inovador que permite a comparação entre serviços ecossistêmicos mensurados com diferentes métricas. A biodiversidade é diretamente dependente da área conservada, mas a produção agrícola pode aumentar sem a necessidade de aumento da área agrícola. Estes resultados mostram que um cenário de ganhos tanto no aumento da produção agrícola como na conservação da biodiversidade são possíveis e devem ser considerados em planejamentos futuros. Em conclusão, o trabalho sugere que esforços de conservação na Floresta Atlântica contemplem os três tipos florestais e priorizem sítios ricos em espécies. A ênfase no aumento da eficiência das práticas agrícolas em terras já convertidas para a agricultura pode promover tanto o incremento da produtividade quanto a conservação da biodiversidade nessa floresta tropical hiperdiversa.

Palavras-chave: Árvore, tropical, comunidade, diversidade, serviços ecossistêmicos.

ABSTRACT

The Atlantic Forest biome is a hotspot of biodiversity and hosts most of Brazil's cultivated land and population. Finding a sustainable path for the land-use in this biome is necessary as regional and global climate conditions, food and energy provision, and biodiversity conservation are all at stake. Applications of the ecological theory can help achieving a sustainable development, reconciling production and conservation in the Atlantic Forest biome. The general objective of this thesis was to verify the pattern of the spatial distribution of the woody species diversity in forest remnants and to relate it with indicators of agricultural production, to subsidize effective conservation actions in the Atlantic Forest. The thesis was organized in three chapters addressing these related topics. The first chapter explored the elements of the metacommunity structure and diversity of the Atlantic Forest and its determinants in different spatial scales. The metacommunity of the entire Atlantic Forest, as well as of its forest types (Ombrophilous Dense, Ombrophilous Mixed, and Seasonal Forests) present a nested subsets structure with grouped loss of species. In addition, the local and geographic components of diversity are responsible for the high diversity of the biome. These results demonstrate that the diversity of the Atlantic Forest is spatially structured and suggests that conservation efforts would be more effective focusing on the protection of diversity-rich sites. In the second chapter, a brief history of agriculture in the Atlantic Forest was presented to show the temporal changes in the agricultural management. The economic exploitation practices of the Atlantic Forest have advanced over the years; it began with an extractivist model, reaching the mechanization and diversification of cultures. The paradigm breach of the agricultural model adopted was one of the responsible for these advances in the Brazilian agriculture. Given the actual levels of threat for the biodiversity, it is suggested that the current moment is a harbinger of a new paradigm in agriculture, with the agricultural advance being based on sustainability. The third chapter explored trade-offs between biodiversity and agricultural production in the Atlantic Forest, using an innovative method that allows the comparison between ecosystem services measured with different metrics. Biodiversity is directly dependent on the conserved area, but agricultural production can increase without the need to increase the agricultural land. These results show that a win-win scenario is possible, conciliating increases in the agricultural production and conserving biodiversity, and should be considered in future land use management planning. In conclusion, the result suggests that conservation efforts in the Atlantic Forest may encompass the three forest types and prioritize sites rich in species. Emphasis on increasing the efficiency of farming practices on already converted lands can enhance both productivity and biodiversity conservation in this hyper-diverse tropical forest.

Key-words: Tropical Forest, metacommunity, tree, diversity, ecosystem services, agriculture.

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SUMÁRIO

1 INTRODUÇÃO GERAL

O Antropoceno é marcado pelo aumento da população humana e da degradação ambiental no planeta. Este fato força a humanidade a encarar o problema fundamental de como suprir as necessidades do homem e, ao mesmo tempo, manter os sistemas que suportam e garantem a vida na Terra (World Commission on Environment and Development, 1987). A ciência da sustentabilidade surgiu nas últimas décadas como esforço de cientistas para responder essa questão (Clark & Dickson, 2003; Clark, 2007). Sustentabilidade pode ser compreendida como a prática de deixarmos para as gerações futuras os múltiplos capitais (estrutural, humano, social e natural) que lhes permitam atingir o bem-estar humano em níveis no mínimo iguais aos da geração atual (Arrow *et al*., 2004; Polasky *et al*., 2015).

Mas, com o aumento da população mundial e do consumo per capita de calorias, há estimativas de que a produção de alimentos precise dobrar nos próximos 35 anos para garantir segurança no suprimento global (Tilman *et al*., 2011). O problema é que o modelo de produção de alimentos amplamente utilizado ao redor do mundo é intimamente atrelado ao desmatamento, que é um dos maiores causadores da emissão de gases do efeito estufa, da perda de biodiversidade e da alteração das características do solo e da água (Leite *et al*., 2012; Chaplin-Kramer *et al*., 2015; Hunke *et al*., 2015). Além disso, existe um interesse crescente em iniciativas de conservação e de restauração dos sistemas naturais a fim de mitigar a perda global de biodiversidade e de serviços prestados pelos ecossistemas (Nazareno & Laurence, 2015). Dessa maneira, parece inevitável que ocorra um pronunciamento ainda maior no conflito entre a demanda de terras para a agricultura e para a conservação da natureza (Smith *et al*., 2010), assim também no debate de como se pode amenizar esse conflito (Latawiec *et al*., 2015).

As Florestas Tropicais do mundo estão no centro desse debate, pois, no geral, apresentam clima e solos favoráveis à produção de alimentos e sistemas naturais hiperdiversos em termos de espécies. Entre 2000 e 2012, essas florestas sofreram grandes perdas de áreas, representando 32% da perda global de cobertura florestal (Hansen *et al*., 2013). Entre as florestas tropicais do mundo, a Floresta Atlântica se destaca como *hotspot* da conservação da biodiversidade, devido aos seus altos níveis de endemismo e, ao mesmo tempo, de degradação ambiental (Myers *et al*., 2003). O bioma Floresta Atlântica abriga a maior parte das terras cultivadas do Brasil e é habitado por mais de 72% da população

brasileira (SOS Mata Atlântica & INPE, 2012). Encontrar um caminho sustentável para o uso da terra na Floresta Atlântica, aliando produção e conservação, se tornou altamente estratégico dado que as condições regionais e globais do clima, a provisão de comida e energia e a conservação da biodiversidade estão todos em jogo (Lapola *et al*., 2014).

O bioma Floresta Atlântica se estende por toda a costa Atlântica brasileira e algumas partes do Paraguai e da Argentina, em latitudes variando entre 5° N a 33°S, longitudes de 35°W a 52°W e altitudes de 0 a 2,200m (Fig.1; Veloso *et al*., 1992). A Floresta Atlântica brasileira cobre uma vasta área (1.481.946 km², aproximadamente 17% do território brasileiro), distribuída em diferentes condições de clima e topografia, abrangendo terras baixas e montanhas costeiras com alta precipitação, bem como planaltos interiores com longos períodos de seca (Oliveira-Filho & Fontes, 2000). Considerando-se a vegetação, as principais fitofisionomias florestais componentes da Floresta Atlântica, aqui referidas como tipos florestais, são a Floresta Ombrófila Densa, a Floresta Ombrófila Mista e a Floresta Estacional Decidual e Semidecidual (Veloso *et al*., 1992). A Floresta Ombrófila Densa é associada ao Oceano Atlântico e se distribui em baixadas (até 50 m acima do nível do mar) e sobre morros e montanhas (50 a 2,200 m a.n.m.) do nordeste ao sul do Brasil (Fig. 1). A temperatura varia entre 22 e 25°C com clima geralmente quente e úmido nas baixadas e frio e seco no topo dos morros (Veloso *et al*., 1992; Oliveira-Filho & Fontes, 2000). A Floresta Ombrófila Mista, também conhecida como Floresta de Araucária por conta da marcante presença da conífera *Araucaria angustifolia*, constitui o principal tipo florestal nos planaltos do sudeste do Brasil, em elevações acima de 500 m a.n.m. (Fig. 1; Hueck 1972). Essas florestas estão em região de clima tropical e subtropical úmido sem períodos pronunciados de seca, com temperaturas médias anuais entre 12°C e 18°C (Behling, 2002). As Florestas Estacionais ocorrem no interior da bacia do rio Paraná no Sul e Sudeste do Brasil (Fig. 1). Essas florestas são caracterizadas por duas estações distintas marcadas por alternância entre clima tropical com chuvas intensas e temperaturas em torno de 22°C no verão, e climas subtropicais com temperaturas baixas, em torno de 15°C, e precipitação escassa no inverno. Grande parte das árvores do dossel dessas florestas são decíduas (20% a 50%), perdendo suas folhas durante períodos frios e secos (Veloso *et al*., 1992) e caracterizando essas florestas como estacionais decíduas e semidecíduas.

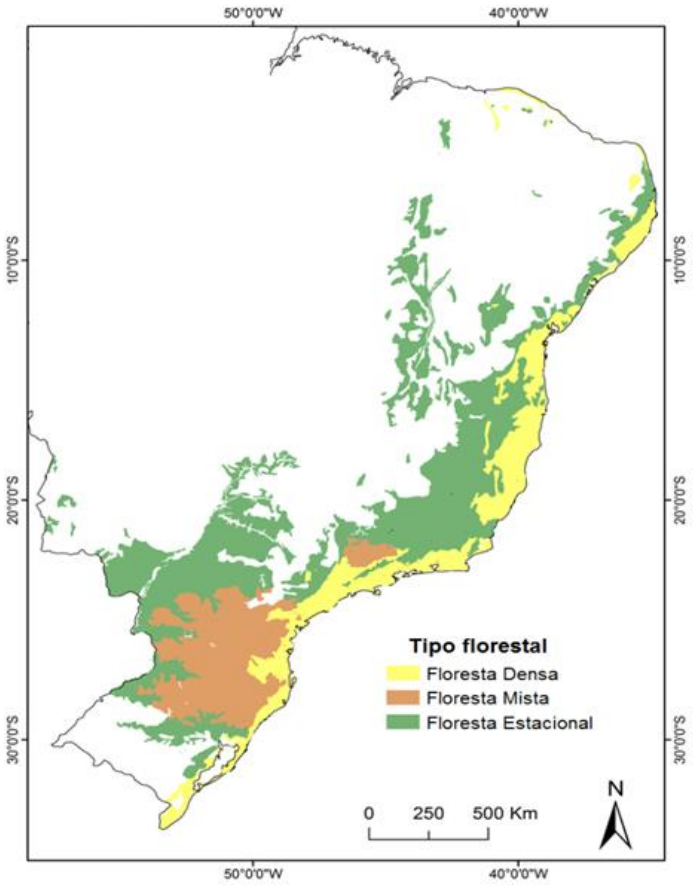

Figura 1. Cobertura original da Floresta Atlântica brasileira dividida em seus tipos florestais (*i.e.*, fitofisionomias florestais *sensu* Veloso *et al*., 1992).

Aplicações da teoria ecológica podem auxiliam nesse objetivo de se atingir o desenvolvimento sustentável do uso da terra na Floresta Atlântica. A avaliação da estrutura de comunidades e dos padrões de distribuição das espécies pode auxiliar no entendimento dos padrões e processos que estruturam a diversidade (Keith *et al.*, 2011; Henriques-Silva *et al.*, 2013; Meynard *et al.*, 2013; de la Sancha *et al.*, 2014; Heino *et al.*, 2015), fornecendo subsídios para práticas eficientes de conservação. Por exemplo, maximizar a conservação em uma metacomunidade de estrutura Clementsiana (Clements, 1916) requer a preservação de comunidades que representem todos os "superorganismos" (*i.e*. todos os grupos de espécies com limites de distribuição discretos) componentes dessa metacomunidade. Por outro lado, em uma metacomunidade com estrutura aninhada, esforços de conservação devem focar em comunidades ricas em espécies, uma vez que estas tendem a conter a grande maioria das espécies que compõem a metacomunidade (Patterson & Atmar, 1986).

Mas não só melhores maneiras de se preservar podem ser fruto da aplicação de

teorias ecológicas. A avaliação do conflito na alocação de terra entre produção agrícola e conservação da biodiversidade (Cavender-Bares *et al*. 2015), por exemplo, pode guiar práticas agrícolas sustentáveis na Floresta Atlântica (Grossman, 2015). Quando o uso da terra não é realizado em sua eficiência máxima, é comum que exista a possibilidade de se aumentar a produtividade agrícola sem sacrificar a biodiversidade (Polasky *et al*., 2012). A aplicação de práticas agrícolas efetivas pode guiar o caminho da sustentabilidade na Floresta Atlântica, conciliando produtividade e lucro com proteção da biodiversidade e manutenção dos ecossistemas.

Essa tese teve como objetivo geral verificar o padrão de distribuição espacial da diversidade de espécies lenhosas em remanescentes florestais da Floresta Atlântica e relacionar com indicadores de produção agrícola, a fim de subsidiar ações eficazes de conservação da biodiversidade neste bioma. A tese foi organizada em três capítulos tratando destes temas relacionados. O primeiro capítulo explorou os elementos da estrutura de metacomunidade e da diversidade da Floresta Atlântica e seus determinantes em diferentes escalas espaciais, com intuito de subsidiar políticas de conservação. Entender como a metacomunidade da Floresta Atlântica como um todo, bem como de seus tipos florestais (Florestas Ombrófila Densa, Ombrófila Mista e Estacional) estão estruturadas, e quais os fatores ambientais são determinantes, podem auxiliar na conservação desse bioma. Além disso, buscou-se evidenciar a contribuição de diferentes componentes da diversidade (alfa, beta) para a diversidade total (gama) da Floresta Atlântica. No segundo capítulo foi apresentado um breve histórico da agricultura na Floresta Atlântica a fim de se evidenciarem as grandes mudanças temporais das práticas agrícolas adotadas, e o papel da quebra de paradigma do modelo agrícola como um dos responsáveis por esses grandes avanços. Considerando as atuais ameaças à biodiversidade, buscou-se discutir a necessidade de um avanço agrícola baseado na sustentabilidade. O terceiro capítulo explorou *trade-offs* entre biodiversidade e produção agrícola na Floresta Atlântica. Foi desenvolvida uma métrica de biodiversidade que combina informação da riqueza de espécies, distinção evolutiva e raridade, em nível local. Verificaram-se os efeitos da alocação de terra e do aumento de eficiência da produção sobre a biodiversidade e sobre o lucro agrícola.

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2 CAPÍTULO I *

ESTRUTURA DE METACOMUNIDADE, PARTIÇÃO ADITIVA E OS DETERMINANTES AMBIENTAIS DA DIVERSIDADE DE PLANTAS LENHOSAS NA FLORESTA ATLÂNTICA BRASILEIRA

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Metacommunity structure, additive partitioning and environmental drivers of woody plants diversity in the Brazilian Atlantic Forest

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spatial scale, biodiversity conservation, elements of metacommunity structure, Dense forest, Mixed forest, Seasonal forest.

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ABSTRACT

Aim To assess the metacommunity structure of woody plants in the Atlantic Forest (AF), compare the structure across its different forest types and evaluate the contribution of multiple scales and environmental drivers for the total biodiversity, providing theoretical basis for efficient conservation of this important *hotspot*.

Location South America, Brazilian Atlantic Forest.

Methods We compiled the occurrence of 2,071 woody plants in 177 sites across the Brazilian AF. We assessed the elements of metacommunity structure (species coherence, turnover and boundary clumping) to identify which idealized structure (checkerboard, nestedness, Clementsian, Gleasonian, evenly-spaced or random) characterizes the AF and its forest types. We used the additive partition of diversity to determine the main spatial scales promoting biodiversity in the AF, i.e. local (within sites, α-diversity), regional (among sites in each forest type, $\beta 1$), or geographical (between forest types, $\beta 2$), and examined environmental variables driving the metacommunity of the AF and forest types using canonical ordinations.

Results The AF and its forest types presented positive coherence, negative turnover and large boundary clumping values which best-fit the *nested subsets* metacommunity structure with clumped species loss. The diversity within sites (α-diversity) and among types ($\beta 2$) was higher than expected by chance. The climatic gradient driving the species composition differed in the AF. Temperature variation affected the entire AF, particularly Dense and Seasonal forests, whereas precipitation affected mostly the Mixed forest.

Main conclusions Despite the similar structure underlying AF metacommunities, the main environmental gradient in each forest differs, highlighting ecological differences among communities at geographical scale. These differences are determinant for the high levels of biodiversity found in the AF. Conservation efforts should encompass all the AF ecosystems, considering its unique characteristics and prioritizing species-rich sites given that they adequately represent the regional species pool.

INTRODUCTION

For over a century ecologists have sought to answer questions regarding the processes that sort species to local assemblages and how they vary across space (Clements, 1916; Gleason, 1926; Diamond, 1975; Tilman, 1982; Ricklefs, 1987; Gaston, 2000; Holyoak *et al*., 2005; Cavender-Bares *et al.*, 2009; McGill, 2014). Studies have shown that processes that promote diversity may change across spatial scales (e.g. Davies *et al*., 2005; Cavender-Bares *et al*., 2009; Silvertown *et al*., 2006; Diez *et al*., 2008; McGill, 2014). Thus, to advance ecology, rather than ask which drivers are most important for biodiversity distribution, we need to understand which drivers are most important at a given spatial scale (Gotelli *et al.*, 2010; McGill, 2014).

The metacommunity concept is an important framework to understand community assembly because it explicitly recognizes that patterns of species distribution and diversity among communities are influenced by both environmental and dispersal processes (e.g., Fernandes *et al*., 2014), and can be applied across different spatial scales (Leibold *et al*., 2004; Presley & Willig, 2010; Meynard *et al.*, 2013). Assessing community structure and species distribution patterns using the metacommunity framework (Leibold & Mikkelson, 2002; Presley *et al*., 2010) have recently helped ecologists to understand patterns and processes structuring diversity (Keith *et al*., 2011; Henriques-Silva *et al*., 2013; Meynard *et al*., 2013; de la Sancha *et al*., 2014; Heino *et al*., 2015). Recent examples include assessments of the relative importance of environmental and spatial properties in species turnover (Henriques-Silva *et al*., 2013; Meynard *et al*., 2013), differences of community structure among clades (Heino *et al*., 2015; de la Sancha *et al*., 2014) and along ecological succession (Keith *et al*., 2011;

Fernandes *et al.*, 2014). In all those studies, the key to understand processes that drive metacommunities is their emergent spatial structure (Presley *et al*., 2010).

As proposed by Leibold & Mikelson (2002) and later expanded by Presley *et al*., (2010), the elements of metacommunity structure (EMS) is a useful framework to assess the underlying processes of metacommunity assembly at different spatial scales (Henriques-Silva *et al*., 2013; de la Sancha *et al*., 2014). The EMS allows identifying which idealized structure (i.e. checkerboard, nestedness, Clementsian, Gleasonian, evenly-spaced or random distributions) best characterizes an empirical metacommunity based in three elements: coherence, turnover and boundary clumping (Leibold & Mikelson, 2002; Fig. 1). The coherence expresses the level in which species are affected by the same environmental gradient; turnover represents the way species composition changes along the gradient, and boundary clumping measures the degree of concordance among the boundaries of the species range along the gradient.

Idealized metacommunities emerging from the combination of these elements present a unique theoretical underpinning (Clements, 1916; Gleason, 1926; Diamond, 1975; Tilman, 1982; Patterson & Atmar, 1986; Presley *et al*., 2010; Dallas, 2014) that facilitates the interpretation of processes regulating the metacommunity and affecting its collective properties (e.g. species richness) (Fig. 1). A checkerboard pattern indicates that multiple pair of species co-occur less than expected by chance (Diamond, 1975). This pattern can arise from various mechanisms that often act in concert, such as interspecific competition, different habitat preferences and dispersal limitation associated to ecological and historical factors (Gotelli & McCabe, 2002; Heino, 2015). Nested metacommunities occur when species in the poorest sites are comprised of subsets of the species found in richer sites and when widely

distributed species present ranges encompassing those of more narrowly distributed species (Patterson & Atmar, 1986). In general, habitat area, isolation and environmental suitability are typical correlates with nestedness (Wright *et al*., 1998). Clementsian gradients consist of communities with tight association among species, behaving like "superorganisms" and presenting discrete community boundaries (Clements, 1916). In contrast, Gleasonian gradients describe communities as mere collections of species, with individualistic responses to underlying environmental gradients, and whose ranges happen to overlap (Gleason, 1926). In evenly-spaced gradients the idealized model of the species range boundaries is hyperdispersed (i.e. the distribution of species ranges is more dispersed than expected by chance) along the underlying environmental gradient (Tilman, 1982), indicating maximal differences among species in environmental tolerances (Presley & Willig, 2010). A random structure characterizes metacommunities in which species respond to different environmental gradients (Presley *et al*., 2010), revealing no coherence among species distributions within the metacommunity. Contrasting these different idealized models simultaneously may reveal more about potential mechanisms that structure metacommunities than studying each model in isolation (Leibold & Mikkelson, 2002; Presley *et al.*, 2011; Meynard *et al.*, 2013; Dallas & Presley, 2014; Heino *et al*., 2015). The metacommunity emergent structure can improve the efficiency of conservation efforts by helping select target areas for biodiversity conservation. For example, maximizing the conservation in a metacommunity with the Clementsian structure (Clements, 1916) requires the preservation of communities that represent all the "superorganisms" (i.e. all the groups of species with discrete distribution boundaries) compounding this metacommunity. On the other hand, in a metacommunity with a nested structure, conservation efforts may focus on richer sites as they tend to contain most species of the metacommunity (Patterson & Atmar, 1986).

Another ecological approach that can improve conservation efforts in a multiscale scenario is diversity partitioning. Biodiversity defined in ecological terms refers to the variety and distribution of species or vegetation types (Noss, 1990) and can be decomposed in three different components: diversity representing the total species pool in a region (γ), within-communities (α) and between-communities (β). This diversity partitioning was originally coined by Whittaker (1960, 1972) and has since been widely used in applied and theoretical ecology, in which several metrics have been developed based on this hierarchical concept (Tuomisto, 2010a,b; Anderson *et al*., 2011). The hierarchical partitioning of diversity is a promising approach to understand patterns of species distribution in compartmentalized systems across spatial scales (Gering *et al*., 2003). It allows analyzing the contribution of each diversity component (α, β) for the total diversity in hierarchical studies with multiscale nested sampling (Lande, 1996) because it identifies the scales in which the diversity is higher or lesser than expected by chance. The hierarchical partitioning of diversity enables evidencing sources of heterogeneity within a megadiverse metacommunity and can provide insights on how conservation efforts could be most cost effective (Gering *et al*., 2003; Summerville *et al*., 2003; Ribeiro *et al*., 2008). Therefore, it is possible to reveal the most important scales contributing for the total diversity in a given metacommunity. Thus, additive partitioning of diversity coupled with description of EMS have the potential to improve our understanding of mechanisms that sort species from the regional pool to local assemblages (de la Sancha *et al*., 2014). In short, EMS allows the characterization of how communities are structured and the diversity partitioning reveal the scales promoting the biodiversity.

The environmental heterogeneity within a metacommunity directly affects its total biodiversity. As the community composition is driven by, among others, the environmental tolerance of each organism (e.g., Weiher & Keddy, 1995), species turnover (β-diversity) is

expected to be higher between areas with different environmental conditions than between areas that have similar environments (Tuomisto *et al*., 2003). Thus, a metacommunity encompassing high environmental heterogeneity also tends to have a higher diversity. Despite this known relationship between the environment and β-diversity, the way in which species composition changes across communities is not necessarily predicted by their differences in environmental conditions. In other words, geographically close metacommunities under different environmental conditions can exhibit either the same or different pattern of species turnover through its main gradient (Henriques-Silva *et al*., 2013; Heino *et al*., 2015). In this way, the knowledge of the metacommunity structure patterns of a heterogeneous and biodiverse system can shed light on processes underlying the relationship between species richness and environmental heterogeneity. Furthermore, it can help conservation efforts as it characterizes how the diversity is distributed and how the environment influences it. This can provide basis for, as example, the choice on how conservation areas should be distributed to maximize diversity.

Given the levels of biodiversity and environmental heterogeneity, the Atlantic Forest (hereafter AF) biome can be a good case study for characterizing biodiversity using the metacommunity approach. The AF is a tropical forest marked by high endemism and intense anthropogenic disturbance, which distinguishes it as a world biodiversity hotspot (Myers *et al*., 2000; Mittermeier *et al*., 2004). It has been defined as a complex biome mainly comprised of three forest types (Brazilian Federal Law 11.428/2006; Oliveira-Filho & Fontes, 2000): the Dense Rainforest, the Mixed Rainforest, and the Seasonal forest. It has been suggested that historical processes related to dispersal limitation and speciation possibly resulted in different phylogenetic structure of communities in each forest type (Duarte *et al*., 2014). Also, previous studies have evidenced rainfall gradients as the major drivers of plant

species turnover in the AF (Oliveira-Filho & Fontes, 2000; Oliveira-Filho *et al*., 2005; Kamino *et al*., 2008; Marques *et al*., 2011; Santos *et al*., 2011). However, it has been shown that different environment factors drive the communities' structures across different AF forest types (Oliveira-Filho *et al*., 2013), such as annual temperature (in Southeastern Dense forest; Oliveira-Filho & Fontes, 2000), duration of the dry season (in Southeastern Seasonal forest; Oliveira-Filho & Fontes, 2000), rainfall seasonality (in Southeastern Seasonal forest; Kamino *et al*., 2008; Santos *et al*., 2011) and soil sandiness (lowland forests within the Southeastern and South Dense Rainforest; Marques *et al*., 2011). However, a link between environmental factors, their imprint on plant metacommunity patterns, and relative importance in different AF types is still needed to better understand the relationship between environmental heterogeneity and the high diversity found in this biome.

To this aim, we used a comprehensive database of tropical trees and shrubs, including the presence-absence of 2,071 species across 177 sites from the Brazilian Atlantic Forest. We applied the EMS framework and the diversity partition approach to determine the community structure and the contribution of each scale (sites, among sites and among forest types) for the high levels of diversity found in the AF. We also assessed the role of climatic variables as drivers of community structure across the entire AF biome and in each of its forest types.

METHODS

The Atlantic Forest biome

The AF extends along the Brazilian coast and a few inland portions of Paraguay and Argentina, originally covering more than one million km². Latitudes range from 5° N to 33° S, longitudes from 35°W to 52°W and altitudes from 0 to 2,200m (IBGE, 1992). This biome

encompasses three different main forest types (Fig. 2). The Dense Rainforests (hereafter Dense Forests) are associated with the Atlantic Ocean and are distributed in lowlands (until 50 m a.s.l.) and slopes (50 to 2,200 m a.s.l.) from northeastern to southern Brazil. Average temperature ranges from 22 to 25°C and the climate is generally hot and wet in lowlands and colder and wetter in the slopes (IBGE, 1992; Oliveira-Filho & Fontes, 2000). Mixed Rainforests (hereafter Mixed forests), also known as Araucaria forests because of the remarkable presence of the conifer *Araucaria angustifolia*, constitutes the main forest type on the highland plateau in southern Brazil at elevations above 500 m a.s.l. (Hueck, 1972). These forests are in regions of tropical and sub-tropical humid climates without pronounced dry periods, where the annual mean temperature ranges from 12°C to 18°C (Behling, 2002). Finally, Seasonal forests are related to the hinterland of the Parana River basin across south and southeast Brazil. These forests are characterized by two distinct seasons with marked alternation from tropical climate with intense rainfalls and temperatures around 22°C in the summer to subtropical climate with lower temperatures around 15°C and scarce precipitation in the winter. Many of its canopy trees are deciduous (20% to 50%), with leaves falling during the colder and drier period (IBGE, 1992), thus characterizing this forest type as semideciduous.

Woody species occurrence in the Atlantic Forest

To compile the checklist of the AF species, we used a comprehensive dataset provided by Bergamin *et al*., (2015) of all published forest surveys from 1994 to 2014 led in the south and southeast of Brazil. We complemented this dataset searching for studies published until March 2015 in all regions encompassing the AF. We considered only studies that used the cutoff diameter at the breast height (DBH) $\geq$ 4.8 cm, in order to standardize the sample

criteria. Our dataset includes a list of 2,071 tree and shrub species from 177 localities (Fig. 2) organized in a presence/absence matrix. The species list was checked for recent synonyms in the Missouri Botanical Garden (http://www.tropicos.org), The Plant List (http://www.theplantlist.org/), and Flora do Brasil databases (http://floradobrasil.jbrj.gov.br), all accessed in February 2016 (Details about the dataset are provided in Appendix S1).

In the compiled dataset, the number of sites and the sampled area in each forest type is proportional to its original cover (Appendix S1). The majority of the AF sites have between 30 to 89 woody species. The total number of species is higher in the Dense forest (S=1,591) compared to the Seasonal (S=1,174) and Mixed (S=683) forests, however, differences among forest types are not statistically significant correcting for sampled area (ANOVA, P=0.068; Fig. 3a,b).

During data compilation we considered only peer reviewed studies and dissertations that used standardized methods. Although we recognize that the dataset may have limitations due to the total number of sites in comparison to the large geographic extent of the AF, the dataset is relatively well-dispersed geographically and proportional to the original cover of forest types. To ensure that sample size was not an issue we repetitively subsampled the data and compared results to the full dataset (see below). Therefore, we are confident that it constitutes a realistic sample of this highly fragmented tropical forest.

Elements of metacommunity structure

Based on three elements of species' distribution in a given metacommunity (i.e. coherence, turnover, and boundary clumping), the EMS analysis determines which idealized metacommunity pattern (Leibold & Mikkelson, 2002), or quasi-structure (Presley *et al*., 2010; Dallas, 2014), best-fits the empirical observation. Incidence matrices were ordinated

via reciprocal averaging, re-arranging sites by similarities in species composition and species by similarities in distribution (Gauch, 1982; Leibold & Mikkelson, 2002). Coherence is assessed statistically by counting the number of embedded absences (i.e., absences within the species range) in the ordination matrix and comparing that value to a null distribution. Turnover is assessed by counting the number of species replacements (see Fig. 1 in Henriques-Silva *et al*., 2013) along the latent gradient and comparing the empirical value to a null distribution (Leibold & Mikkelson, 2002). Boundary clumping is evaluated by comparing the observed distribution of range boundaries with an expected equiprobable distribution (Hoagland & Collins, 1997; Leibold & Mikkelson, 2002; Presley *et al*., 2010). Furthermore, the pattern of species loss in nested structure can be distinguished through boundary clumping (Fig. 1) and each pattern is analogous to evenly-spaced, Glesonian, or Clementsian structures, except that the range boundaries' dispersion is only in one direction of the gradient (for more details, see the discussion of Leibold & Mikkelson, 2002 and Presley *et al*., 2010).

We used the 'Metacommunity' function of 'metacom' package (Dallas, 2014) implemented in the R environment (R Core Team, 2014). We adopted a highly conservative null model (fixed-fixed) that holds constant the number of species on each site and fill species occurrences among sites at random, but maintains the number of occurrences observed for each species (Ulrich & Gotelli, 2007). The results of coherence and turnover were expressed as *Z*-scores and boundary clumping by the Morisita's index (Morisita, 1971). All null models were based on 1,000 permutations. Furthermore, to check whether the number of sites affected the EMS results, we subsampled 28 sites randomly from the Dense and Seasonal forests (i.e., the same number of sites as the Mixed forest) and performed the EMS analysis on each iteration (Appendix S2).

Additive partitioning of diversity

We tested the uniformity of species diversity (S) across spatial scales using the additive partitioning of total diversity (Lande, 1996), which considers that mean alpha (α) and beta (β) diversities add up to gamma (γ) diversity. Thus, β-diversity is measured in the same biodiversity dimension as α and γ, defined here as species richness (S) (Lande, 1996). This additive procedure is then extended across multiple scales in a hierarchical sampling design with *i = 1, 2, 3, …, m* levels of sampling (Crist *et al*., 2003), which in our case was: local (within sites, α-diversity), regional (among sites in each forest subtype, β1), and geographical (between subtypes, β2). Samples in lower hierarchical levels are nested within higher level units (ex.: sites are nested within forest types and forest types are nested within the AF). At each level *i*, αi denotes the average diversity found within samples. At the highest sampling level, the diversity components are calculated as:

$$\beta m = \gamma - \alpha m$$

For each lower sampling level as:

$$\beta i = \alpha(i+1) - \alpha i$$

Then, the additive partition of diversity is:

$$\gamma = \alpha 1 + \sum \beta i$$

Average alpha components (α_m) are uniformly weighted to calculate it as simple average. The

expected diversity components are calculated 999 times by individual based randomization of the community data matrix.

We computed the additive diversity partitioning in the R environment (R Core Team, 2014) using the function "adipart" (follows Crist *et al*., 2003) from the 'vegan' (version 2.0-8) package.

Environmental drivers of species composition

We used canonical correspondence analysis (CCA; TerBraak, 1986) to determine which environmental variables were associated with species composition and underlying metacommunity structure of the AF and its forest types. The CCA axes are defined by reciprocal averaging, which is the same ordination method used to identify the main gradient of species distribution in the EMS framework (de la Sancha *et al*., 2014). It is a powerful method for determining associations among environmental variables and the metacommunity structure, indicating its main drivers (de la Sancha *et al*., 2014). We also performed a PCA analysis with the same dataset, to compare the main drivers of variation among these ordination procedures. We used the 19 bioclimatic variables available in the WorldClim data base (http://www.worldclim.org/), at a spatial resolution of 5', as environmental factors (Hijmans *et al*., 2005). These variables include annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation) and extremes (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters of years). We also used the latitude and longitude coordinates in the CCA analyses as surrogates for unmeasured spatially-structured environmental variables. CCA and the PCA were conducted in the R environment with the "cca" and "princomp" functions, respectively, from the 'vegan' package (R Core Team, 2014; Oksanen *et al*., 2013).

RESULTS

Elements of metacommunity structure

Surprisingly, both the metacommunity defined by the entire AF and separately by forest types exhibited a nested structure with clumped species loss, characterized by positive coherence, negative turnover and large values (>1) of boundary clumping (Table 1). The positive coherence suggests that species are responding to the same environmental gradient in the metacommunity. The significant negative turnover indicates that species composition changes less than expected by equiprobable distributions. The boundary clumping pattern shows that changes in community composition occur by clusters of species. The observed patterns did not change after controlling for sample size, with the nested structure being corroborated as the best fit (Appendix S2).

Additive partitioning of diversity

For the total woody species' diversity (γ = 2,071 species), the hierarchical partitioning showed that each site (α), on average, retains more diversity than expected by the null hypothesis - that assumes equity among scales ($P< 0.001$, Fig. 4). The β-diversities among sites within forest types ($\beta 1$) are lower than expected by chance ($P< 0.001$). On the other hand, the observed among-forest type β diversities ($\beta 2$) were higher than expected by the null hypothesis ($P< 0.001$).

Environmental drivers

The metacommunity of both the AF and Dense forest were generally structured by similar environmental drivers (Table 2). Their EMS ordination axis were positively related to Temperature Seasonality and negatively related to cold temperatures (e.g., Min Temp of

Coldest Month and Mean Temperature of Coldest Quarter) whereas precipitation variables were less important (Table 2). The metacommunity structure of Seasonal forest followed the same trends of both AF and the Dense forest but with a lower number of variables showing strong correlations (Table 2). Finally, Mixed forest showed a negative relationship with Temperature Seasonality and a stronger relationship with precipitation variables compared to the other forest types (Table 2). Moreover, for all forest types the metacommunity structure was related to the sites' spatial distribution (latitude and/or longitude), but negatively for AF, Dense and Seasonal forests and positively for Mixed forest structure. The CCA (Appendix S3) and PCA (Appendix S4) results present similar patterns of the relationship between each variable and the first axis of variation.

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DISCUSSION

The AF is a continental biome where tree species' distributions and processes of community assembly are affected by different factors and mechanisms acting at different scales. At the

biome scale, the emergent metacommunity structure comprised of nested subsets of species correlated mostly with temperature. We found this structure pervasive across forest types, but while species composition in Dense and Seasonal forests was determined mainly by temperature, precipitation variables were more important in the Mixed forest. This difference leads to high species diversity on a geographical scale (among forest types).

The AF presented the same idealized metacommunity structure at the biome and geographical (forest types) scales. This indicates that the species composition changes in a similar way along the main gradient at different spatial scales (Meynard *et al*., 2013). The nested structure presented by the AF and all forest types is a structure in which the species of species-poor sites represent subsets of species found in species-rich sites (Leibold & Mikkelson, 2002). In other words, this structure evidences that the ranges of species with restricted distributions along the environmental gradient are contained within the ranges of widely-distributed species (Presley *et al*., 2010). The nested structure also indicates that the communities have some degree of similarity in species composition, which is corroborated by the lower than expected beta-diversity within forest types ($\beta 1$). Indeed, Eisenlohr & Oliveira-Filho (2015) showed that around 30% of the species occurring in a given AF forest type are common to the entire AF, and approximately 40-55% of the species of a given AF forest type are not restricted to that type.

A nested subset structure may arise due to different factors operating at local and regional scales such as metacommunity biogeographical factors (i.e. species probability of extinction, colonization and speciation) as well as some filters that species need to pass in order to establish in a site (i.e. sampling filter, distance filter, habitat filter, and area filter; see Wright *et al*., 1998 for details). Given that we evaluated the AF metacommunity from the species

range perspective (see Presley *et al*., 2010 for a discussion on this matter), we believe that the nested structure detected here may be due to the nested habitat hypothesis (Hylander *et al*., 2005). In short, this hypothesis predicts that all species within a metacommunity have the optima of their realized niche on the same end of the main gradient. The nested structure arises due to differences in each species capability of establishing along non-optimal parts of this gradient (Hylander *et al*., 2005). Therefore, the nested structure of the AF's communities suggests that they are composed of species with different tolerances, from environmental generalist with wide distributions, to specialist with narrow environmental and geographical ranges.

It is worth noting that the AF and its forest types do not constitute perfect nested systems as some species are restricted to specific sites and the metacommunity structure presented a pattern of clumped species loss. These patterns are probably due to similarities of species' environmental requirements and dispersal, which reflected in association among species' geographic distributions (Presley *et al*., 2010). This can shade light as to why, even with lots of species with restricted distribution (~22% of each forest type composition), the best predicted metacommunity structure that fits the AF and its forest types is the Nested subset structure.

Temperature-related factors were found to be the main drivers of the entire AF woody plant metacommunity. De la Sancha *et al.*, (2014) also found temperature as the main driver of AF small mammals' metacommunity structure, emphasizing the importance of temperature gradients as a driver of species composition in the AF. This contradicts, in part, results from previous studies (Oliveira-Filho & Fontes, 2000) that found precipitation as the major driver of Southeastern AF structure at the species level whereas temperature was important at the

genus and family levels. However, disentangling this forest complex and analyzing each forest type separately revealed that the Mixed forest distinguishes from the others by presenting an opposite relationship with temperature seasonality and being mainly affected by precipitation factors. Species composition of the Mixed forest is remarkably influenced by the presence of basal clades of woody plants (Duarte *et al*., 2014) that are characterized by limited water efficiency (Feild *et al*., 2002; Boyce *et al*., 2009; Brodribb & Field, 2010) and thus constrained by water availability (Duarte, 2011). Taken together, these facts may explain why precipitation was found to be a major driver of the Mixed forest metacommunity structure and stress the singularities of each forest type comprising the AF biome.

The relation between the main structure of the AF metacommunity as well as its different forest types with geographic location (latitude and longitude) reveals the role of spatially structured factors on the species composition. Previous researches on the Southeastern AF (Oliveira-Filho & Fontes, 2000; Eisenlohr & Oliveira-Filho, 2015) have shown that the distance from the sea influences floristic composition. The Brazilian coastal mountain range *Serra do Mar* and the inland plateau create a relatively abrupt relief transition from coastland to hinterland. This altitudinal transition is related to changes in climatic factors, including temperature, frost events, atmospheric pressure, solar radiation, air masses speed and rainfall patterns (Jones, 1992). The moist air masses from the Atlantic Ocean face a barrier on the coastal mountain range and sudden changes in atmospheric pressure and air speed leads the greater part of these air masses to precipitate over the *Serra do Mar* seaward side. This coastland region has the highest mean annual rainfall of the entire AF range (up to 3,600 mm), while in the inland plateau, with typical seasonal climates, mean annual rainfall ranges from 1,300 to 1,600 mm (Oliveira-Filho & Fontes, 2000).

Our findings also indicate that the main processes promoting biodiversity act at local (site) and geographical (among forest types) scales. The number of species within sites (α) and the turnover of species between forest types (β_2) maintain the high diversity in the AF. The high β2 diversity can be related to the environmental heterogeneity, as suggested by the variation found in the environmental drivers among forest types. Also, the high species turnover between the AF forest types (β2) can be due to their distinct biogeographic history as suggested by their contrasting phylogenetic patterns (Duarte *et al*., 2014). The high α diversity indicates that the communities in the AF, in general, are composed of more species than expected by chance. At this small scale, microclimate variation and species interactions are hypothesized to play major roles in the process of community assembly (Cavender-Bares *et al*., 2009; McGill, 2014).

Implications for conservation

The results presented in this study bring valuable information for the conservation of this biodiversity hotspot. As social and economic constraints limit the possibility of conservation of all the remaining AF, it is crucial to identify and apply the limited resources in locations where biodiversity conservation is maximized. The nested metacommunity structure characterized in this study suggests that conservation would be most effective if efforts were focused on protection of biodiversity rich sites (Hylander *et al*., 2005) given that they contain most species from poorer sites. However, it is important to recognize that many species are regulated by metapopulation dynamics, such that they may need more than populations co-occurring on richer sites to survive on the long term (Hanski, 1998). Furthermore, while the metacommunity structure underlying all the AF is similar, many species have different environmental requirements and restricted distributions associated to forest types. This

highlights the ecological differences between communities at the geographical scale and adds to the understanding of the high levels of biodiversity found in the AF. Many factors need to be accounted in effective conservation of biodiversity (Margules & Pressey, 2000), our results suggest that conservation efforts should consider species rich sites, encompass all the forest types and their unique characteristics to complement and maximize biodiversity in the Atlantic Forest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Dataset detailed information.

Appendix S2 Effects of the number of sites on the EMS analysis.

Appendix S3 CCA plots for the entire AF, and for the Dense, Mixed and Seasonal forests.

Appendix S4 PCA plots for the entire AF, and for the Dense, Mixed and Seasonal forests.

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TABLES

Table 1. Elements of Metacommunity Structure (EMS) for the entire Brazilian Atlantic Forest (AF) and each forest type (Dense, Mixed, Seasonal). These metrics combined best fit a nested structure with clumped species loss for the entire AF and separately for forest types.

Forest	Coherence (*Z* score / *P* value)	Turnover (*Z* score / *P* value)	Boundary Clumping (Morisita's index / *P* value)
AF	2.42 / 0.0154	-3.90 / <0.0001	7.06 / <0.0001
Dense	2.48 / 0.0130	-2.97 / 0.0029	7.94 / <0.0001
Mixed	2.00 / 0.0447	-2.56 / 0.010	2.56 / <0.0001
Seasonal	2.01 / 0.0438	-3.10 / 0.0019	5.70 / <0.0001

Table 2. Loadings of the first axis from CCA for entire Atlantic Forest (AF) and separately for each forest type, based in latitude, longitude and BioClim variables. In bold, correlations ≥0.70.

Variables	AF	Dense	Mixed	Seasonal
Latitude	**-0.85**	**-0.89**	**0.74**	-0.64
Longitude	**-0.87**	**-0.90**	0.69	**-0.78**
Temperature				
Annual mean temperature	**-0.72**	**-0.80**	-0.03	-0.61
Mean diurnal range temperature	0.69	0.66	0.44	0.60
Isothermality	-0.55	**-0.76**	0.67	-0.35
Temperature Seasonality	**0.85**	**0.91**	**-0.70**	0.68
Max Temperature of Warmest Month	-0.26	-0.39	-0.36	-0.17
Min Temperature of Coldest Month	**-0.88**	**-0.89**	-0.21	**-0.81**
Mean Temperature of Wettest Quarter	-0.39	-0.27	0.40	-0.43
Mean Temperature of Driest Quarter	**-0.83**	**-0.89**	-0.10	-0.66
Mean Temperature of Warmest Quarter	-0.54	-0.58	-0.30	-0.42

Mean Temperature of Coldest Quarter	**-0.82**	**-0.88**	0.22	**-0.73**
Precipitation				
Annual Precipitation	0.01	0.05	0.07	**0.74**
Precipitation of Wettest Month	-0.03	0.08	0.62	0.17
Precipitation of Driest Month	0.12	0.07	-0.64	0.47
Precipitation Seasonality	-0.14	-0.09	**0.73**	-0.36
Precipitation of Wettest Quarter	-0.06	0.08	0.64	0.21
Precipitation of Driest Quarter	0.13	0.05	-0.65	0.49
Precipitation of Warmest Quarter	0.38	0.57	0.64	0.54
Precipitation of Coldest Quarter	-0.49	**-0.73**	**-0.71**	0.35

FIGURES

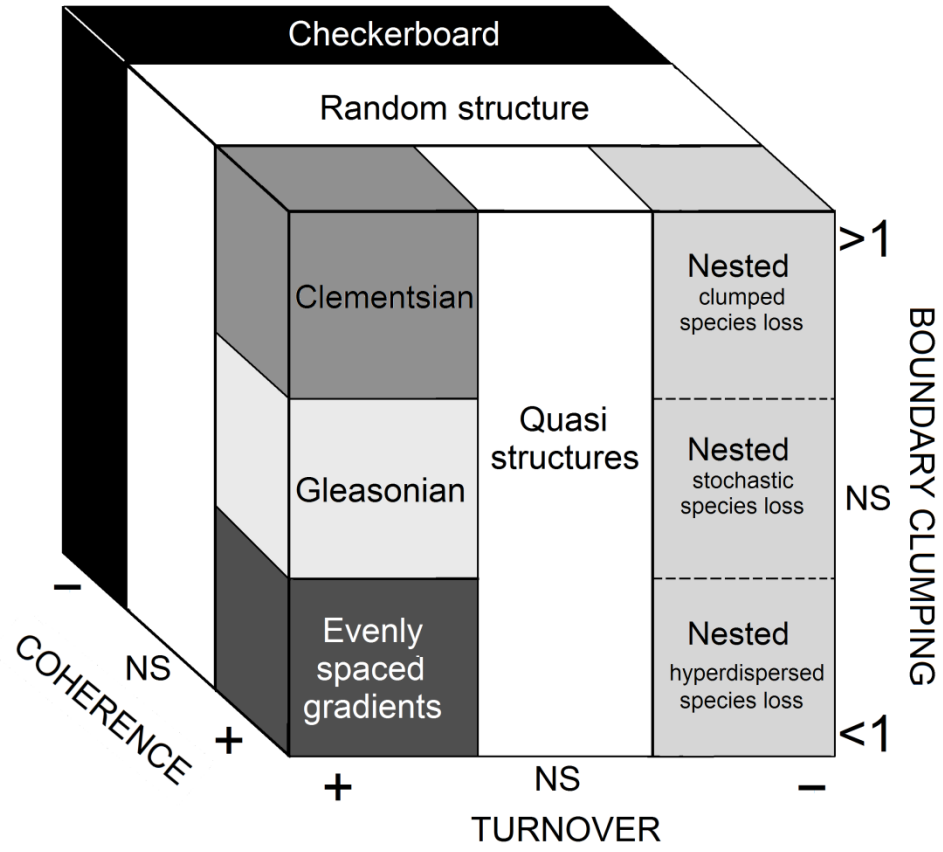

Figure 1. A three-dimensional space formed by the three attributes used to identify metacommunity structure (coherence, turnover and boundary clumping; adapted from Dallas 2014). NS denotes *P* value higher than 0.05. Every area of this cube is related to an idealized structure, quasi structure or random structure. The pattern of species loss within nested subset structure is also discriminated. This cube permits easily linkage between elements of metacommunity structure metrics and the respective structure. Furthermore, it also allows the visualization of the relation between the possible structures in the three-dimensional space.

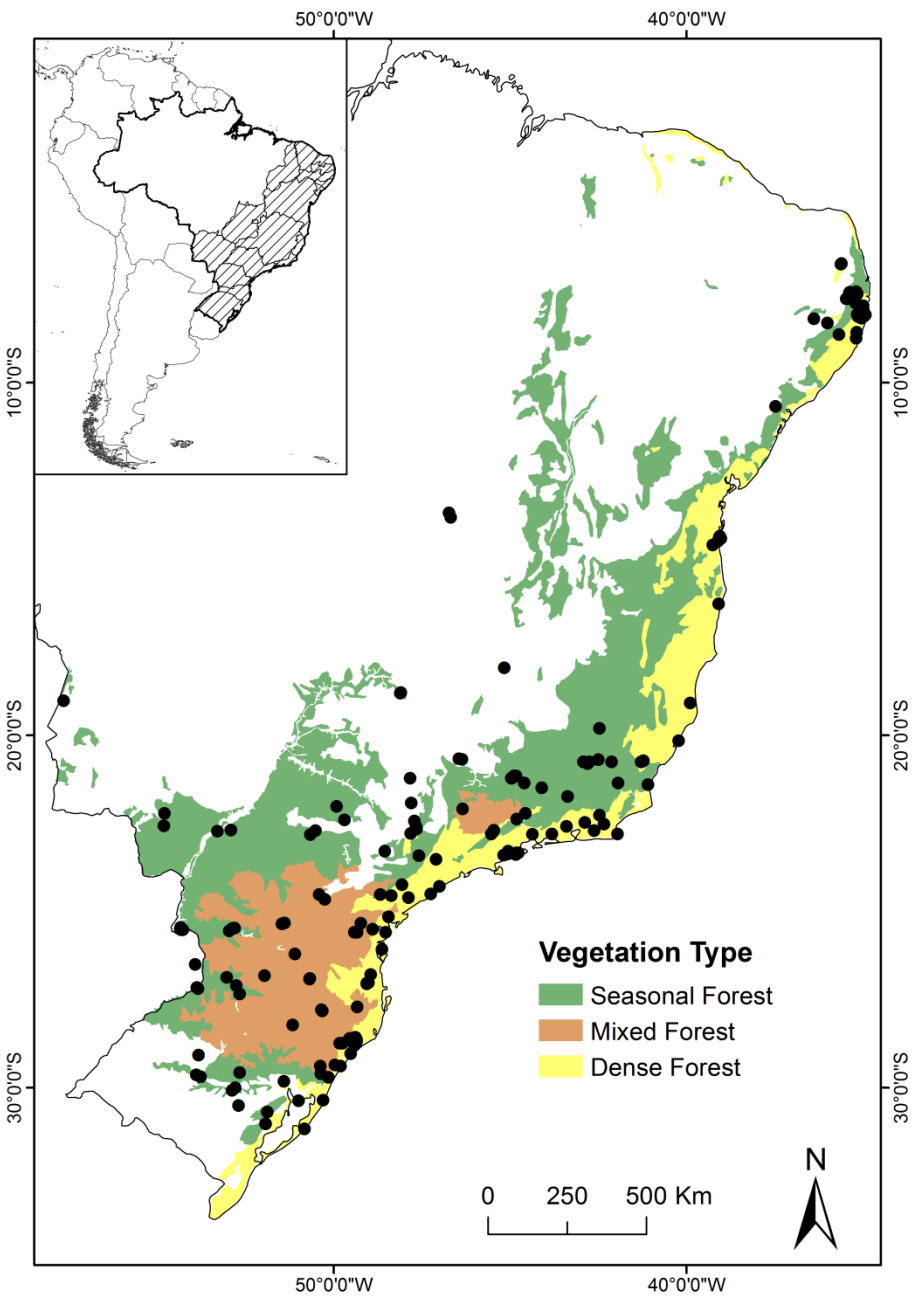

Figure 2. Map of the Brazilian Atlantic Forest biome distribution on the South America continent (shaded area in the small map), and the natural covering area of each forest type (by color in the main map). The black dots represent the location of all 177 sites compounding our dataset.

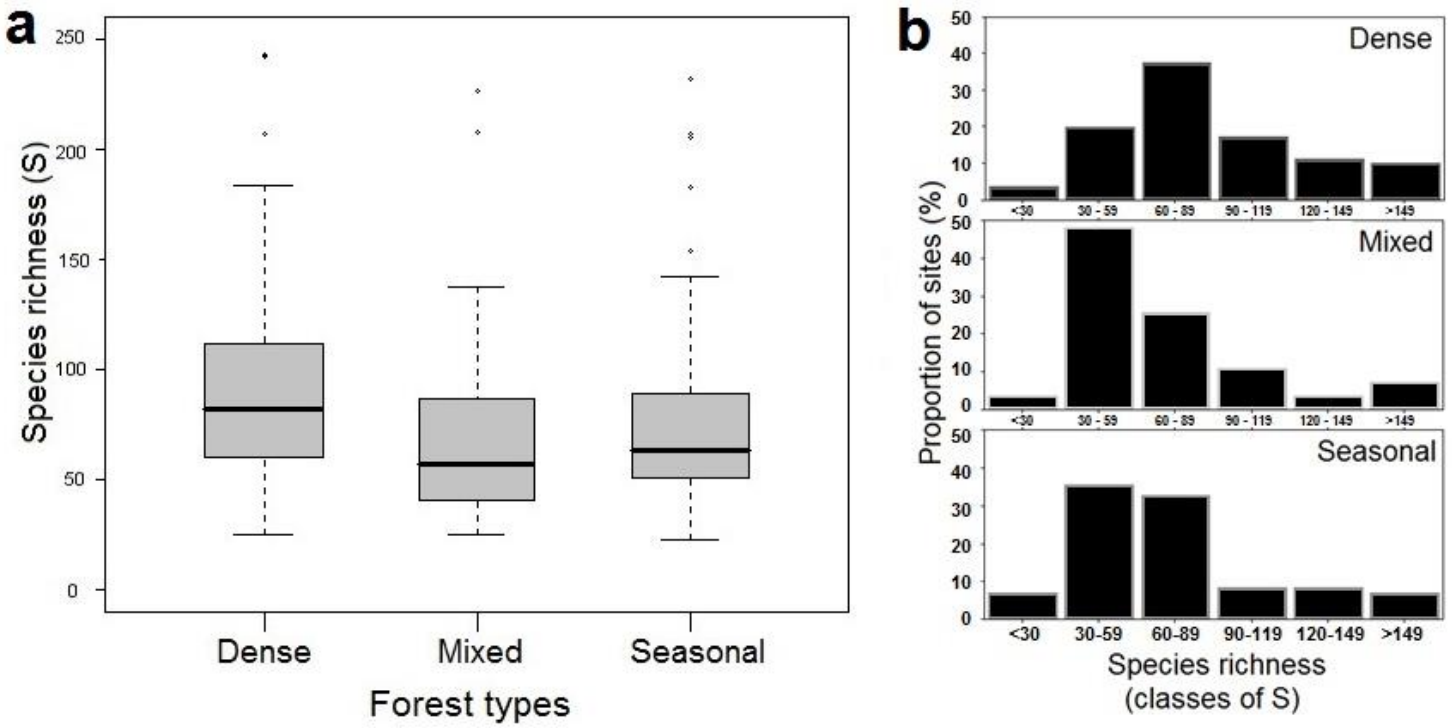

Figure 3. (a) Boxplot of the average species richness per site for the Atlantic Forest types; (b) histogram of the proportional number of sites in each class of richness for the Atlantic Forest types.

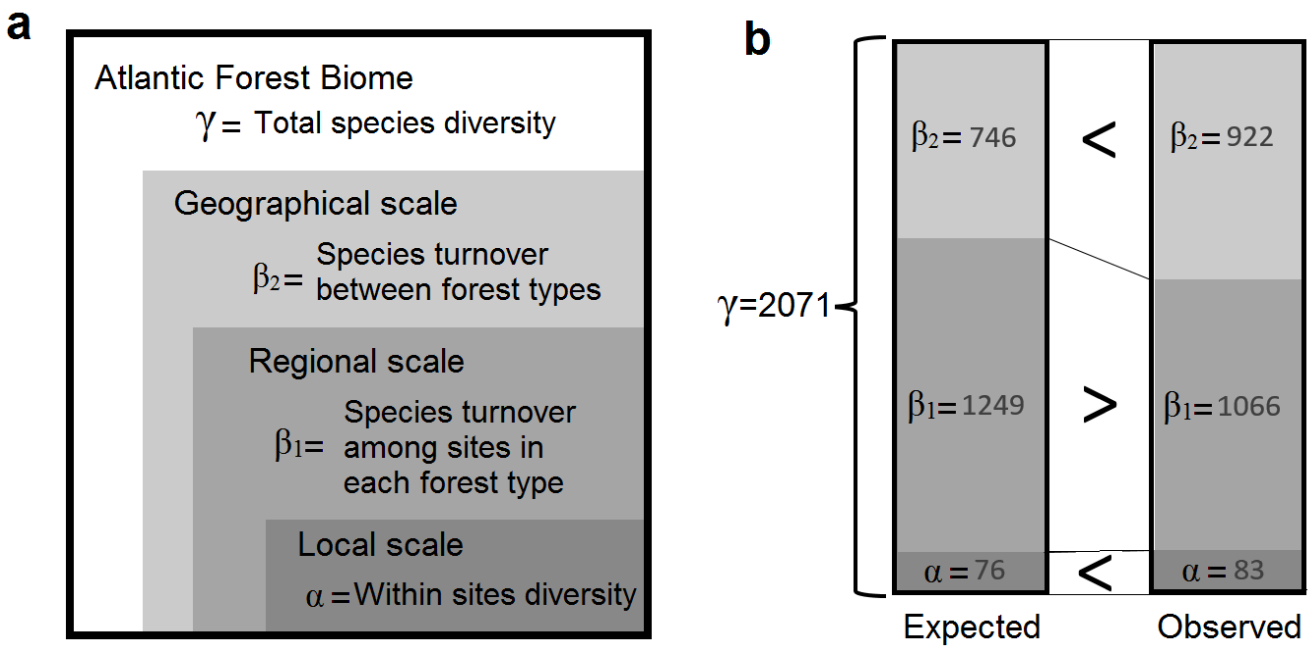

Figure 4. (a) the associations between the spatial scale analyzed (geographical, regional and local) and each diversity component (α, β_1, β_2 and γ), note that the additive partitioning explicitly considers the hierarchy among the spatial scales; and (b) the graphical representation of the additive partitioning of the Atlantic Forest species diversity in the different diversity components. The algebraic symbols denote the differences between partition values expected by chance and the observed values. All the observed values are different (P<0.001) from that expected in a mean of 1,000 random distributions (for more details, see Methods).

3 CAPÍTULO II

AGRICULTURA E BIODIVERSIDADE: NOVOS PARADIGMAS PARA A CONSERVAÇÃO DA FLORESTA ATLÂNTICA

Agricultura e biodiversidade: novos paradigmas para a conservação da Floresta Atlântica

O bioma Floresta Atlântica, um *hotspot* de biodiversidade extremamente degradado (Myers *et al*., 2003), abriga a maior parte das terras cultivadas do Brasil, e é habitado por mais de 125 milhões de pessoas (Lapola *et al*., 2014). Neste bioma estão inseridas extensas áreas urbanas como as áreas metropolitanas de São Paulo e do Rio de Janeiro, as duas maiores cidades brasileiras. Das áreas originais de floresta, restam apenas 12% (~160000 km²) e menos da metade deste percentual estão em áreas protegidas (SOS Mata Atlântica & INPE, 2012). Por cobrir a costa Atlântica brasileira, fato que lhe rendeu o nome, a Floresta Atlântica foi a primeira a receber iniciativas de colonização no Brasil. A presença do homem foi fator crucial para a redução em mais de dez vezes da área original desse bioma. Atualmente, cientistas (Lapola *et al*., 2014; Strassburg *et al*., 2014; Phalan *et al*., 2016; Alves-Pinto *et al*., 2017; Marcilio-Silva *et al*., in prep; entre outros) buscam formas de mudar esse paradigma de que o desenvolvimento econômico e rural venha às custas da destruição da natureza.

Neste trabalho fazemos um apanhado de como as mudanças na economia e agricultura estiveram historicamente associadas ao desmatamento da Floresta Atlântica. A partir destes dados discutimos a atual situação do bioma e as possíveis formas de promover uma nova mudança que alie a sustentabilidade na produção agrícola com a conservação dos seus remanescentes.

Breve histórico da Agricultura na Floresta Atlântica

O historiador Warren K. Dean (1996) descreveu a história da Floresta Atlântica nos últimos séculos como marcada pela devastação: “uma história de exploração e destruição”. A Floresta Atlântica não existe mais em sua extensão e forma originais, tanto por causa dos séculos ou milênios de agricultura indígena, quanto por causa das décadas pós-colonização europeia, com a industrialização acelerada de um Estado colonial e burguesia com ideais de desenvolvimento econômico rápido e irresponsável (Dean, 1996). Assim, índios, caboclos, colonos, latifundiários, grandes industriais, Estado, todos tiveram certa cota de responsabilidade na destruição desse bioma. Embora alguns destes grupos tenham feito essa

exploração de forma relativamente equilibrada durante longos períodos de tempo (*e.g.*, grupos indígenas), outros desenvolveram formas predatórias e em larga escala de exploração da Floresta Atlântica, como é o caso dos colonizadores europeus que chegaram ao continente sul americano no século XV (Dean, 1996).

Da Floresta Atlântica saíram as primeiras riquezas a serem exploradas pelos portugueses e, desde então, vários ciclos importantes de extração e produção se desenvolveram no seu domínio. No início da colonização, as riquezas naturais do Brasil não se revelaram promissoras. O extrativismo do pau-brasil (que deu origem ao nome do país) na região da Floresta Atlântica foi a primeira razão econômica da posse das então novas terras por Portugal, e o corte seletivo dessa árvore foi um dos primeiros grandes impactos dos colonizadores sobre a floresta (Arruda, 1996). Logo o foco da então colônia passou a ser a extração de metais preciosos, o que impulsionava o comércio internacional por meio das exportações marítimas (Prado Junior, 2006). A introdução da cana-de-açúcar na região Nordeste ocorreu em 1533, já no início da colonização do Brasil, mas somente com o desenvolvimento da colônia no final do século XVI essa cultura ganhou proporção importante para a economia colonial. A conversão da floresta em áreas agrícolas, principalmente na região Nordeste, já tomava grandes proporções. Neste período, a cana-de-açúcar tornou-se o principal produto agrícola negociado, garantindo fomentação e incremento à economia nacional. Assim, mudou-se o paradigma da economia na então colônia, saindo da exploração direta de produtos florestais e minerais para se iniciarem cultivos agrícolas. O cultivo de cana-de-açúcar estimulou os colonizadores europeus a introduzirem a mão-de-obra escrava, como retratado na imagem de um engenho da época (Piso, 1648; Fig. 1). Os escravos realizavam duras tarefas inerentes ao cultivo dessa monocultura, e o tráfico negreiro, nessa época, gerou elevados lucros para os comerciantes de escravos e também, através de impostos, para a coroa portuguesa. A concentração de riqueza e a formação de latifúndios geraram um sistema social quase feudal no Brasil, diferentemente do que ocorreu, por exemplo, na América do Norte, onde a terra foi dividida em pequenas propriedades. As terras brasileiras permaneceram em situação de colônia explorada por longo período de tempo, garantindo a Portugal o acúmulo de riquezas oriundas do cultivo e beneficiamento da cana-de-açúcar, principalmente cultivada na região Nordeste, obtendo grande disseminação no mundo e proporcionando à coroa portuguesa, por algum tempo, hegemonia ante ao mercado mundial (Holanda, 1995). As pressões sobre a floresta cresciam juntamente com o

desenvolvimento agrícola e social da então colônia. Mas a economia brasileira era dependente da exportação do açúcar e não possuía acesso direto aos mercados, que eram controlados pelos holandeses, vindo a declinar na segunda metade do século XVII (Baer, 2003). Nesse período, muitas regiões produtoras de açúcar passaram então a diversificar sua produção, introduzindo culturas como o fumo e o cacau, na Bahia. O algodão, produzido principalmente no Maranhão e no Grão-Pará, teve um crescimento temporário, guiado pela Guerra da Secessão (1861 - 1865) nos Estados Unidos da América (Baer, 2003).

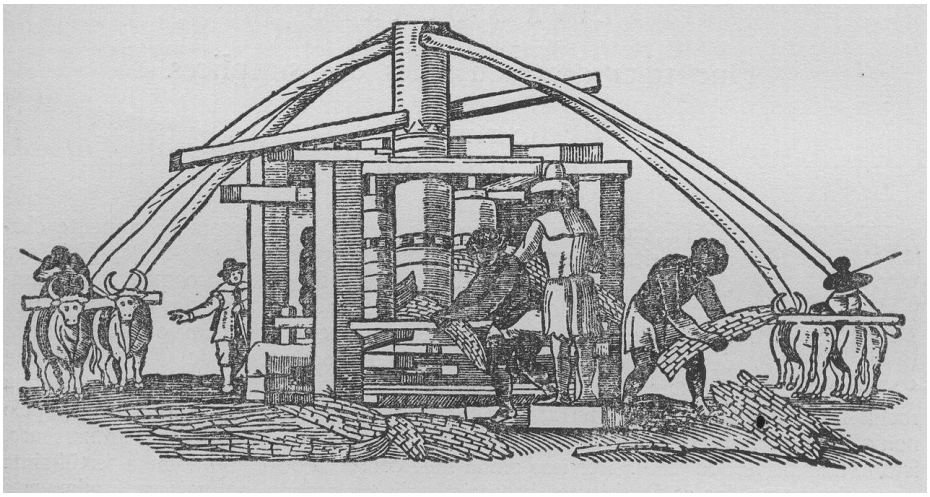

Figura 1. Retratação de um engenho de açúcar na obra *Historia Naturalis Brasiliae* de Guilherme Piso, 1648.

Ainda no final do período colonial, em meados de 1730, o cultivo de café foi introduzido no Brasil. Mas foi somente após a independência do país, em 1822, que a produção se consolidou na região Sudeste, sobretudo no estado de São Paulo. A exportação do café, iniciada no século XIX, passou a ter enorme peso econômico, fazendo surgir uma nova oligarquia dominante no Brasil, os chamados Barões do Café (Baer, 2003). Nesse período, grandes áreas de Floresta Atlântica já estavam convertidas em áreas agrícolas e urbanas, tanto na região Nordeste quanto Sudeste. Com o fim da escravidão no final do século XIX, a demanda por mão-de-obra na produção de café apressou os movimentos de imigração, sobretudo de europeus, acentuados com a produção do café no oeste de São Paulo. O ciclo do café durou até a crise econômica global de 1929, encerrando-se, sobretudo no Rio de Janeiro e São Paulo, na década de 1930. Nesse período, o capital oriundo do excedente cafeeiro possibilitou a industrialização do país (Arruda, 1981).

Aproximadamente na metade do século XX, teve início no Brasil um debate que indicava o atraso no setor agrícola como um dos obstáculos ao desenvolvimento e à

industrialização do país. Com esse atraso de modernização, a agricultura não atendia mais à demanda dos grandes centros urbanos, e cidades como São Paulo, Rio de Janeiro e Recife sofriam com escassez de gêneros básicos como açúcar, trigo e feijão (Ortega & Nunes, 2001). O uso de maquinário agrícola no Brasil ainda era tão raro nessa época que tratores e colheitadeiras eram utilizados em desfiles pelo interior (Fig. 2). No meio acadêmico, duas correntes se debatiam, uma dizendo que o país possuía uma estrutura feudal no campo, defendida por intelectuais conservadores como Oliveira Viana (historiador e sociólogo), e outra, defendida por intelectuais como Prado Junior (historiador e político), criticando a estrutura rural capitalista. Ambas visões pregavam a reforma agrária como meio de melhora do sistema econômico e sugeriam a necessidade de alterações na Constituição para reverter esta situação. Esse quadro gerou oposição acirrada por parte da ala conservadora da sociedade. A instabilidade econômica e social do Brasil nesta época culminaram no Golpe Militar de 1964 (Ortega & Nunes, 2001).

Figura 2. Agricultores desfilando com suas máquinas agrícolas no então povoado de Mauá no Rio Grande do Sul, em 1962 (foto de Roberto Brudna, disponível em https://mbrudna.wordpress.com).

Durante o regime militar no Brasil, foi criada em 1973 a EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária), com objetivo de diversificar a produção agrícola do país. O órgão foi responsável pelo desenvolvimento de novos cultivares, adaptados às condições peculiares das diversas regiões do país. Teve início, então, a expansão das fronteiras agrícolas com latifúndios monocultores produzindo soja, algodão e feijão em escala

semi-industrial. As políticas de fomento agrícola incluíam créditos subsidiados, perdão de dívidas bancárias e subsídios à exportação que chegavam a 50% do valor do produto. Novamente uma mudança de paradigma ocorreu no país, dessa vez no sentindo de diversificação das culturas e mecanização do trabalho no campo. Assim, entre 1960 e 1990 ocorreu um grande avanço na agricultura brasileira: os produtos agrícolas exportados passaram de quatro para dezenove e produtos agrícolas beneficiados que representavam apenas 16% do total exportado passaram a representar 80% (Baer, 2003).

Já após o fim do regime militar e com a democratização, a partir de 1994, com a estabilização monetária gerada pelo plano Real, o modelo agrícola brasileiro passou por grandes mudanças. O Estado diminuiu sua participação e o mercado passou a financiar a agricultura, fortalecendo a cadeia do agronegócio. A liberação do comércio exterior com a diminuição das taxas de importação dos insumos, entre outras medidas, forçaram os produtores brasileiros a se adaptarem às práticas de mercado globalizado. O aumento da produtividade em geral, a mecanização e profissionalização marcaram esse período (Baer, 2003). Essa substituição da mão de obra por máquinas reduziu a população rural brasileira de 21,7 milhões em 1985 para 17 milhões em 1995, e aumentou o número de tratores no país, de 665 mil para 803 mil no mesmo período (IBGE, 2006). Essas tendências da agricultura no Brasil se mantiveram no início do século XXI. A população rural continuou diminuindo e, em 2006, apenas 16 milhões de pessoas estavam ocupadas no campo. Nesse mesmo ano, o Brasil dispunha de 60,6 milhões de hectares de lavouras, entre culturas temporárias e permanentes, e uma frota de 820 mil tratores (IBGE, 2006).

O resultado de todos os ciclos econômicos pelos quais o Brasil passou foi a conversão quase que total da Floresta Atlântica original (SOS Mata Atlântica & INPE, 2012). Mesmo apresentando pressões diferentes sobre a vegetação nativa, cada ciclo contribuiu para a antropização aguda desse bioma, sendo guiado pelas necessidades do país na época (Tab. 1). Apesar da observação de que as taxas de desmatamento terem sido reduzidas nas últimas décadas (Dias *et al*., 2016), a devastação e fragmentação dos remanescentes da Floresta Atlântica nunca pararam.

A necessidade de práticas agrícolas sustentáveis

O Brasil é um país com alta capacidade para aumentar sua produtividade agrícola, tendo, no geral, clima favorável e vastas áreas com grande potencial para a agricultura.

Atualmente, as atividades agrícolas são os principais causadores do desmatamento da Floresta Atlântica brasileira (Gibbs *et al*., 2010). O problema é que o desmatamento é um dos maiores causadores da emissão de gases do efeito estufa, da perda de biodiversidade e da alteração das características do solo e da água (Leite *et al*., 2012; Chaplin-Kramer *et al*., 2015; Hunke *et al*., 2015). O histórico da agricultura no país revela os padrões da contínua conversão dos biomas brasileiros nas últimas décadas (Lapola *et al*., 2014; Dias *et al*., 2016). Hoje, a Floresta Atlântica abriga a maior parte da população brasileira e apresenta em torno de 90% de sua área antropizada, convertida principalmente em áreas agrícolas (Metzger, 2009; SOS Mata Atlântica & INPE, 2012). A importância econômica das áreas agrícolas e sua produção são evidenciadas no fato do Brasil estar entre os dez primeiros exportadores globais de produtos agrícolas (FAO, 2012), sendo o setor agrícola responsável por 25% do produto interno bruto (PIB) nas últimas duas décadas (Lapola *et al*., 2014). Além disso, é esperado que a produção e exportação dos produtos agrícolas brasileiros continuem seu ritmo de crescimento nos próximos anos (Dias *et al*., 2016).

Com o aumento da população mundial e do consumo per capita de calorias, há estimativas de que a produção de alimentos precise dobrar nos próximos 35 anos para garantir segurança no suprimento global de comida (Tilman *et al*., 2011). Neste cenário, a intensificação da produção agrícola na região da Floresta Atlântica é inevitável, mas não necessariamente associada à expansão da fronteira agrícola. Apesar de não ter desaparecido completamente, a ligação entre expansão agrícola e desmatamento segue enfraquecendo no país (Lapola *et al*., 2014). Por exemplo, a produção brasileira de grãos dobrou desde 2005 mesmo com a diminuição do desmatamento no Brasil nesse mesmo período (Dias *et al*., 2016). Uma das principais estratégias propostas para garantir a segurança global de produção de alimentos é a intensificação sustentável da agricultura (Rudel *et al*., 2009; Lapola *et al*., 2014; Strassburg *et al*., 2014). Essa estratégia visa o aumento da produção agrícola sem aumento de área destinada à agricultura ou aumento da degradação ambiental. Strassburg *et al*. (2014) demonstraram que o Brasil tem potencial para aumentar a produtividade pecuária permitindo a conversão de pastagens em áreas agrícolas, possibilitando uma produção agrícola sustentável até 2040. Apesar de a agricultura brasileira ser historicamente extensiva (*i.e.*, agricultura praticada em grandes extensões de terra, em geral com baixos investimentos em tecnologia e nenhuma especialização, apresentando baixa produtividade por área) com expansão de áreas agrícolas à custa da vegetação natural, dados dos últimos anos indicam a

diminuição da extensificação e aumento na intensificação (*i.e.*, agricultura que utiliza tecnologia, mecanização e especialização da mão de obra, apresentando alta produtividade por área) da agricultura no país (Dias *et al*., 2016). Mesmo sendo ainda pouco expressiva no cenário nacional, a intensificação pecuária e agrícola no Brasil já é uma realidade e o país está acima das médias globais neste quesito (FAO, 2012; Lapola *et al*., 2014).

Para garantir um futuro que combine segurança alimentar e proteção da natureza, a expansão de áreas agrícolas no Brasil precisa parar por completo (West *et al*., 2014). Algumas peculiaridades do Brasil (*i.e.*, clima e solo favoráveis a diversas culturas agrícolas, regulação do mercado interno, aumento de áreas protegidas, controle do desmatamento ilegal, entre outras) o colocam em posição única para a intensificação da sua produção agrícola sem aumentar o desmatamento (Lapola *et al*., 2014; Phalan *et al*., 2016). É um dos poucos países no planeta com chances de alcançar tanto a proteção de seus *hotspots* de biodiversidade quanto alta produtividade agropecuária (Martinelli *et al*., 2010; Alves-Pinto *et al*., 2017), indicando o grande potencial do país para o desenvolvimento sustentável.

É necessário mudar o pensamento comum de que maior produtividade significa simplesmente maior produção de alimento, mas sim que a intensificação nas áreas agrícolas já estabelecidas possibilita que outras áreas sejam destinadas à conservação da biodiversidade (Phalan *et al*., 2016). Essa visão sustentável traz um novo paradigma para o uso do solo em países tropicais altamente dependentes da agricultura, mas que ainda possuem grandes frações da biodiversidade global em suas florestas (Lapola *et al*., 2014). Mesmo sendo ainda pouco expressiva no cenário nacional, a intensificação pecuária e agrícola no Brasil já é uma realidade e o país está acima das médias globais neste quesito (FAO, 2012; Lapola *et al*., 2014).

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Tabela 1. Diferentes ciclos econômicos históricos do Brasil, seus efeitos sobre a Floresta Atlântica e alguns fatores que colaboraram com as mudanças de paradigma em cada época.

Ciclo	Período de início	Situação do Brasil na época	Pressão sobre a Floresta Atlântica	Região principal	Fatores de mudança
Extração do Pau Brasil[1,2,6]	Início do século XI	Colônia de Portugal	Corte seletivo	Costa Atlântica brasileira; Floresta Ombrófila Densa	Necessidade do desenvolvimento econômico e estabelecimento da colônia
Cana-de-açúcar[2,5,6]	Final do século XI	Colônia de Portugal	Conversão das áreas naturais em áreas agrícolas e urbanas	Nordeste (principalmente Pernambuco e Bahia); Floresta Ombrófila Densa e Floresta Estacional	Falta de acesso direto aos mercados e competição internacional
Café[,1,3,5]	Inicio do século XIX	Independência e primeiro reinado	Conversão das áreas naturais em áreas agrícolas e urbanas	Sudeste e Sul: São Paulo e Rio de Janeiro (Vale do Paraíba) e Paraná (terras roxas do norte); Floresta Ombrófila Densa, Floresta Ombrófila Mista e Florestas Estacionais	Necessidade de suprir a demanda interna de produtos agrícolas e desenvolver a economia do país. Atraso do setor agrícola perante outros países
Diversificação das culturas e mecanização da produção agrícola[1,5,6,7]	Final do século XX	Final do regime militar e início da Nova República	Conversão de áreas naturais em áreas agrícolas, consolidação e expansão de áreas urbanas	Todo Brasil, consolidação das áreas agrícolas e urbanas em toda Floresta Atlântica e avanço maior sobre o Cerrado e a Amazônia	Necessidade global e regional de desenvolvimento sustentável da agricultura / Oportunidade de inovação

FONTE: [1] Arruda, 1981; [2] Prado Junior, 2006; [3] Holanda, 1995; [4] Arruda, 1996; [5] Ortega & Nunes, 2001; [6] Baer, 2003; [7] Lapola *et al*., 2014.

É necessário mudar o pensamento comum de que maior produtividade significa simplesmente maior produção de alimento, mas sim que a intensificação nas áreas agrícolas já estabelecidas possibilita que outras áreas sejam destinadas à conservação da biodiversidade (Phalan *et al*., 2016). Essa visão sustentável traz um novo paradigma para o uso do solo em países tropicais altamente dependentes da agricultura, mas que ainda possuem grandes frações da biodiversidade global em suas florestas (Lapola *et al*., 2014). A intensificação sustentável da agricultura no Brasil poderia manter o aumento previsto da produção e, ao mesmo tempo, parar a degradação da Floresta Atlântica e dos outros biomas brasileiros. Melhorias na tecnologia e nas práticas agrícolas visando a intensificação ou implementação de novos sistemas de produção podem resultar em um cenário "ganho-ganho", conciliado proteção da natureza com produção de alimentos, mostrando que a sustentabilidade é algo que pode ser atingida (Tab. 2). Mas, atingir essa intensificação sustentável no Brasil será um enorme desafio político, tecnológico e social (Lapola *et al*., 2014; Strassburg *et al*., 2014; Phalan *et al*., 2016; Alves-Pinto *et al*., 2017). Para se alcançar a sustentabilidade, não somente a aplicação de técnicas já desenvolvidas em outros países e/ou experimentalmente no próprio Brasil são necessárias, mas uma mudança na própria visão da agricultura por parte dos produtores e de toda sociedade brasileira. O papel dos tomadores de decisão é crucial para esse fim, desde a elaboração e aplicação de leis que protejam os remanescentes florestais, fomento a agências que subsidiem a experimentação e a aplicação das práticas agrícolas sustentáveis até as diretrizes da Educação no país. Como ponto de partida, é essencial que os tomadores de decisão tenham disponíveis informações acuradas sobre os padrões da produção agrícola e das características naturais dos remanescentes não antropizados no país, bem como o conhecimento de técnicas e abordagens de intensificação sustentável da agropecuária. Tendo por base a ciência (tecnologias e práticas em inovação constante), o produtor rural e toda a sociedade brasileira podem encontrar formas eficazes e harmônicas para conjugar os verbos produzir e preservar.

Tabela 2. Estudos indicando práticas agropecuárias sustentáveis possíveis para o Brasil e para a Floresta Atlântica, e os principais desafios inerentes à suas aplicações.

Atual uso da terra	Caminho para a sustentabilidade	Desafios	Região	Fonte
Sistemas agropecuários extensivos e de baixa diversidade	Adoção de sistemas integrados "agrícola-pecuário-florestal"	Aplicação em larga escala do conhecimento desenvolvido em fazendas experimentais	Brasil	Bungestab 2012
Pecuária extensiva	Intensificação sustentável da pecuária e conversão de parte das áreas de pastagem em áreas agrícolas	Planejamento na alocação da terra, melhoria na aplicação da lei, monitoramento e garantia da posse da terra	Brasil	Strassburg *et al*., 2014
Produção de cana-de-açúcar	Diminuição de emissões de gases do efeito estufa na produção de cana-de-açúcar	Prevenção da degradação e erosão do solo, proteção das bacias hidrográficas e erradicação da expansão sobre os remanescentes florestais	Floresta Atlântica	Filoso *et al*., 2015
Agricultura extensiva	Implementação de sistemas agroflorestais, identificação de espécies nativas com potencial de uso não-madeirável	Melhoria na aplicação da lei, disponibilidade local e oportunidades de mercado dos produtos não-madeiráveis	Floresta Atlântica	Oliveira & Carvalhaes 2016
Pecuária extensiva	Intensificação sustentável da pecuária, incremento da apicultura e do turismo rural	Melhorias na disponibilidade e qualidade da mão de obra, aumento da assistência técnica e diminuição da resistência cultural	Floresta Atlântica	Alves-Pinto *et al*., 2017
Agricultura extensiva	Intensificação sustentável da agricultura	Planejamento na alocação da terra, aumento da assistência técnica e diminuição da resistência cultural	Floresta Atlântica	Marcilio-Silva *et al*., in prep

Conclusão

Infelizmente a alta biodiversidade da Floresta Atlântica tem sido anualmente perdida. A pressão sobre este bioma é imensa e sua conservação de extrema importância. Desde seu primeiro contato, o homem tem explorado a riqueza dessas florestas de maneira predatória. Mas as práticas de exploração econômica da Floresta Atlântica avançaram muito ao longo do desenvolvimento do Estado brasileiro. Em vários momentos desta história, a quebra de paradigma do modelo agrícola utilizado bem como a aplicação de novas tecnologias trouxeram grandes avanços para a agricultura no Brasil. Mais uma vez o modelo agrícola brasileiro precisa avançar e agora em direção à sustentabilidade. Felizmente, o país possui condições favoráveis a esse objetivo, e já mostra indícios de trilhar esse rumo. O uso de aplicações teóricas e tecnologias de ponta deve ajudar no alcance desse objetivo de aumentar ambos, produtividade agrícola e conservação da natureza. Isto torna urgente a demanda por conhecimentos científicos que possam subsidiar melhores práticas de conservação e de intensificação da produção agrícola. Somente com estes poderemos atingir a sustentabilidade e deixar para as gerações futuras as mesmas condições e oportunidades disponíveis às gerações atuais, conciliando segurança alimentar e proteção da biodiversidade.

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4 CAPÍTULO III*

AVALIANDO OS *TRADE-OFFS* ENTRE BIODIVERSIDADE E PRODUÇÃO AGRÍCOLA NA FLORESTA ATLÂNTICA

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Assessing the land use trade-offs between tree biodiversity and crop production in the Atlantic forest

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ABSTRACT

Sustainability science has emerged as a problem-driven field aimed to address the fundamental problem of meeting human needs while maintaining Earth's life support systems. Within this context, trade-offs in ecosystem services (ES) have received increasing attention because provisioning services that meet human needs in the short term often come at the expense of regulating, cultural, or supporting services. However, when realized land-use patterns are not at their maximum efficiency it is often the case that provisioning services can be increased without sacrificing other ecosystem services or biodiversity, enabling a "win-win" scenario. The Atlantic Forest (AF) is a hotspot for biodiversity conservation, given its high level of endemism, as well as the levels of threat it faces from human land-use change. In this context, examining trade-offs between biodiversity and crop production in the AF can provide insights to decision makers about land-use management. We developed a biodiversity metric that combines information on species richness, evolutionary distinctiveness, and rarity, at the local level. Then, we examined the extent to which the three different forest types within AF differ in the nature of ES trade-offs. Furthermore, we assessed how annual deforestation rates and different land management affects plant biodiversity and agricultural revenues. Finally, we tested whether it is possible to achieve the same total regional revenue without reducing biodiversity, by improving local management practices. The three forest types show similar patterns in ES trade-offs, with slight differences within Mixed forest due its high evolutionary distinctiveness. Our results reveal that biodiversity is likely to be more sensitive to land use change than crop revenues: certain crops can yield up to ten times more in some sites compared to others, such that by enhancing management practices, it may be possible to increase revenues without reducing biodiversity. Taken together, we show that human well-being can be enhanced without further conversion of Atlantic Forest. However, achieving management outcomes that increase efficiency by maintaining higher biodiversity and increasing provisioning services depends on 1) knowledge of forest type, 2) the fit or comparative advantage gained from planting crops in the best places, and 3) preserving species in a balanced manner across forests.

Key Words: Ecosystem services; Atlantic forest; sustainability; biodiversity; conservation; land-use; deforestation; cropland

INTRODUCTION

Increasing human population and environmental degradation in the Anthropocene Era forces humanity to confront the fundamental problem of how to meet human needs while maintaining the Earth's life support systems (World Commission on Environment and Development 1987). Sustainability science has emerged in the last decades to address this question (Clark and Dickson 2003, Clark 2007). One widely held view of sustainability defines it as leaving to future generations multiple kinds of capital (manufactured, human, social, and natural) that will allow them to maintain human well-being at a level at least as high as that of the current generation (Arrow et al. 2004, Polasky 2015). With respect the ecosystem services (ES) that foster Earth's life support systems, land use trade-offs arise because provisioning services (e.g., food production, wood and fiber, fuel) that meet human needs in the short term often come at the expense of regulating (e.g., flood regulation, water purification, climate regulation), cultural (e.g., aesthetic, educational, recreational, spiritual), or supporting (e.g., nutrient cycling, soil formation, primary production) services (Millennium Ecosystem Assessment 2005), which are critical to well-being in the long-term. As humans increase the extraction of provisioning services, regulating and supporting services decline with negative consequences for the supply of ES in the future (Tilman et al. 2002, Zhang et al. 2007, Nelson et al. 2008, Cavender-Bares et al. 2015a).

However, despite this general land use trade-off between provisioning and regulating ecosystem services, when realized land-use patterns are not at their maximum efficiency it is often the case that provisioning services can be increased without sacrificing regulating ecosystem services or biodiversity (Polasky et al. 2008, Polasky et al. 2012, Cavender-Bares 2015b). Examination of ecosystem service trade-offs across a range of systems around the globe have consistently revealed that better management policies and land-use practices can

allow for greater efficiency in landscape-level output of goods for human consumption without compromising regulating and supporting services (Faith et al. 1996, Egoh et al. 2010, Cavender-Bares et al 2015b, Ewing and Runck 2015, González-Esquivel et al. 2015, Grossman 2015). Therefore, effective management practices that enhance the efficiency of provisioning services at high levels of other ES, can allow a "win-win" scenario in which productivity and revenues can increase while biodiversity and ecosystems are sustained.

The high demand by decision makers for assessment of trade-offs between ecosystem services led scientists to create and advance several tools for this purpose (Faith and Walker 1996, UK National Ecosystem Assessment 2011, Kline and Mazzotta 2012, Smith et al. 2012, White et al. 2012, Cavender-Bares et al. 2015a). Cavender-Bares et al. (2015a) proposed a simple integrated framework for the analysis of these trade-offs. This approach does not require that services necessarily be represented in terms of the common monetary metrics, but can directly show trade-offs between different services measured in their own terms. It allows direct comparisons between provisioning services, commonly measured in monetary values, with regulating, cultural and supporting ecosystem services, less frequently measured in monetary values, or other attributes of ecosystems of importance to humans, such as biodiversity.

Despite challenges in measuring regulating, cultural and supporting services, biodiversity can be considered a good surrogate for them (Mace et al. 2012), given its known role in driving ecological functionality and services (Hooper et al. 2005, Balvanera et al. 2006, Rey Benayas et al. 2009). Biodiversity also has intrinsic value that many humans care about and represents our Earth's biological heritage in a manner that is often considered an important cultural service (Maris 2010, Díaz et al. 2015). However, biodiversity (all living variation, from genes to ecosystems) itself presents multidimensional characteristics

(Lyashevska & Farnsworth 2012). The simple number of species in a site does not directly reflect their genetic diversity nor the evolutionary history represented among coexisting species. As a consequence, Faith et al. (2010) argued that an evolutionary perspective is essential not just for a more comprehensive description of biodiversity, but also for assessing ecosystem services trade-offs and providing a better understanding of the links between biodiversity and human well-being. However, a broader conservation goal should not rely only on maximizing phylogenetic diversity but integrating it with other prioritization criteria. (Larkin et al. 2016). Furthermore, the rarity of a given species in a given system should matter for analyses of trade-offs as it can represent the vulnerability of species to local or regional extinction. The local loss of a regionally common species affects the regional species pool less than the loss of a very rare species, which can lead directly to regional extinction and a possible loss of ecosystem services (Maina and Howe 2000). Incorporating the number of species, the evolutionary distinctiveness of those species and their rarity, we describe trade-offs between biodiversity and provisioning ecosystem services, more comprehensively than simply counting species, and we examine how alternative metrics of biodiversity influence analyses of trade-offs with provisioning services.

The Atlantic Forest in South America is a hotspot for biodiversity conservation, given its high level of species endemism and richness, as well as the increasing levels of threat it faces from human land-use change (Mittermeier et al. 2004). This widespread tropical forest encompasses three connected forest types (Oliveira-Filho and Fontes 2000): the Dense Rain Forest, the Mixed Rain Forest and the Seasonal Deciduous and Semideciduous Forest. Prior to European settlement, the Atlantic Forest covered the Brazilian Atlantic coast inwards to eastern Paraguay and Northeastern Argentina. Since the 1500's, with the arrival of Europeans, the Atlantic Forest has been increasingly converted to open space for the

establishment of croplands/pastures and villages/cities. Currently, the Atlantic Forest region hosts nearly 70% of the Brazilian population, and less than 12% of the original forest cover still stands (SOS Mata Atlântica and INPE 2009). The Brazilian law that should ensure the native vegetation protection (Native Vegetation Protection Law – NVPL; Law #12,651 from 2012) should be considered based on both scientific and juridical knowledge to foster a better balance between urban expansion, and agricultural production, on the one hand, and biodiversity conservation and ecosystem services provisioning, on the other (Brancalion et al., 2016). Furthermore, the expansion of agriculture, which provides commodities that the Brazilian economy depends on, is the main driver of deforestation (Gibbs et al., 2010). Foley et al. 2011 have argued that a sustainable future, which integrates both food security and environmental protection, depends on circumscribing agriculture to limit the habitat loss and environmental damage.it causes. In the face of alarming increases in habitat and biodiversity loss, the Brazilian government ratified world-wide goals for biodiversity conservation (Convention on Biological Diversity 2010). In alignment with these goals, the Brazilian ministry of environment is implementing a national plan to restore native vegetation (PLANAVEG 2014; available at www.mma.gov.br/images/arquivo/80049/Planaveg/PLANAVEG_20-11-14_copy.pdf) that seeks to restore at least 12.5 million hectares of forests (4±0.3 Mha of Atlantic Forest) over the next 20 years.

Targeted lands for restoration are largely privately owned rural properties not in compliance with the NVPL, which requires preservation or restoration of native vegetation on at least 20% of the area of their land in the Atlantic Forest region. Scientific data and projections indicate that currently planned restoration will not affect the production and supply of food, fiber and fuel, allowing provisioning ES to keep increasing following the

trends of past decades (Brancalion et al. 2012, Sparovek et al. 2012). However, there is a widely held perspective, mainly among rural producers, that the conservation plan constrains agricultural development in Brazil. Furthermore, in an analysis of agriculture land use patterns in Brazil, Dias et al. (2016) highlight the importance of understanding the interactions among ecosystem services, agricultural productivity and expansion of agricultural land area. Here we examine these interactions and assess how current conservation plans would likely impact both agricultural provisioning services and biodiversity.

Our first objective is to develop a biodiversity metric that combines information on species richness, evolutionary distinctiveness, and rarity, at the local level that is thus more comprehensive in addressing multiple conservation criteria than species richness, alone (e.g., Larkin et al. 2016). Our proposed biodiversity conservation (BC) index summarizes multiple components of biodiversity (richness, phylogenetic distinctiveness, and rarity) at multiple scales. To examine the extent to which the different individual metrics of biodiversity impact the resulting trade-off patterns, we compare biodiversity and provisioning ES trade-offs using individual biodiversity components, analyzed separately, or summarized jointly in the BC metric. Second, we examine the extent to which the three different forest types within Atlantic Forest differ in the nature of biodiversity and provisioning ES trade-offs. We hypothesize that trade-off curves will differ among the forest types as a consequence of their climatic, edaphic, historical and geographic differences. Third, we assess how annual deforestation rates in the Atlantic Forest affect biodiversity and agricultural revenues for each forest type. We hypothesize that increased deforestation caused by expanding cropland area will have a greater proportion impact on biodiversity than on revenue (calculated as a proportion of current levels). Fourth, we compare how crop revenues and biodiversity are

likely to change under three different plausible scenarios of land allocation to agricultural production and conservation in private lands of the Atlantic Forest region. We hypothesize that biodiversity will be more sensitive to changes in land allocation under these contrasting land use scenarios than agricultural revenues. Finally, we examine the potential for improved management to increase local revenues without negatively impacting biodiversity. We test whether it is theoretically possible to achieve the same total regional revenue without reducing biodiversity, by improving local management practices within each municipality.

METHODS

The Brazilian Atlantic Forest

The Atlantic Forest originally covered more than one million square kilometers along the oriental Brazilian lands, in both, coastal and inland areas (Mittermeier et al. 2004) where the three different forest types are distributed. The Dense Rain Forest (Dense Forest) is associated with the Atlantic coast and includes areas of lowland (until 50 m a.s.l.) and slope (50 to 2,200 m a.s.l.) forests from the Northeastern to the Southern regions of Brazil. The climate is generally hot and wet in lowlands and cold and wetter in slopes and the temperature ranges between 22 and 25ºC (IBGE 1992, Oliveira-Filho & Fontes 2000). The Mixed Rain Forest (Mixed Forest) is also known as Araucaria Forest because of the remarkable presence of the conifer *Araucaria angustifolia*; constitute the main forest type on the highland plateau in Southern Brazil at elevations above 500 m a.s.l. (Hueck 1972). This forest is in region of tropical and sub-tropical humid climates without pronounced dry periods and the annual mean temperature ranges mainly from 12°C to 18°C (Behling 2002). Seasonal Rain Forest (Seasonal Forest) is related to the hinterland Parana River basin in the South and Southeast Brazil and with the transition between the Dense Forest and the Caatinga (deciduous, thorny, xerophytic inland vegetation) in the Northeastern region. The Seasonal

Forest is characterized by two distinct seasons with marked alternation from a summer with intense rainfalls and temperatures around 22ºC to a winter with low temperatures (around 15ºC) and scarce precipitation. This forest is characterized as semideciduous as not all but many of its canopy trees (20% to 50%) fall their leaves (deciduous) during the cold and dry period (IBGE 1992).

Woody species occurrence

We use the comprehensive dataset provided by Bergamin *et al*. (2015) for our list of the Atlantic forest species, which includes 206 floristic checklists describing the occurrence of 1,916 woody species (details in Bergamin et al. 2015). We complemented this checklist by searching studies from March to December 2015 using the same search criterion as Bergamin *et al*. (2015). We used the entire plant list (3,145 species in 414 sites) to generate the species pool to develop the phylogeny used for the calculation of the evolutionary distinctiveness (details below). We used a subset of this list, including only sites with sampling criteria of DBH $\geq$ 4.8 to generate the matrix describing the presence/absence of 2,071 species (columns) at 177 sites (rows) for all the remaining analysis.

In the analyzed dataset, the number of sites in each forest type is proportional to the original cover area for each forest type. From the total area originally covered by Atlantic Forest (1,233,875 km²), Dense forest represented 44%, Mixed forest 16% and Seasonal forest 40% (Bullock et al. 1995, SOS Mata Atlântica and INPE 2009). Of the 177 sites included in our dataset, 80 sites are within the Dense Forest area (45%), 27 in the Mixed Forest (15%) and 70 in the Seasonal Forest region (40%). Our sampling thus appropriately reflects the proportion among forest types in the original Brazilian Atlantic Forest.

Provisioning service dataset

We generate an estimate of provisioning services for all the Atlantic Forest municipalities present in our data set (125 municipalities in total) by assessing available information about all plant-based food production. We searched for the cropland area, yield, market price and production cost for all crops (annuals and perennials) provided by the Brazilian Geography and Statistics Institute (IBGE; http://cidades.ibge.gov.br/) and the Brazilian Agricultural Research Corporation (Embrapa; https://www.embrapa.br/) websites during May-July 2015. We constructed a dataset describing each municipality by the production area of each crop, total cropland income and total income and costs per crop type. We compiled the available data for all years from 2010 to 2013 in order to capture interannual fluctuation in productivity and market prices. A total of 125 municipalities, 20 perennial crops and 18 annual crops were included the dataset.

Biological Conservation Index

We developed the Biological Conservation (BC) index for summarizing different biodiversity dimensions of a site in a single metric. The BC takes in account species richness, species rarity and phylogenetic distinctiveness of each site. Species richness was calculated as the total number of species in the site. The evolutionary distinctiveness (ED) (or phylogenetic distinctiveness) was calculated using the function "evol.distinct" in the package picante (Kembel et al. 2010). The ED is a phylogenetic topology based measurement in which the species values are calculated as the sum of values per phylogenetic branch (Isaac et al. 2007). The branch value is its length divided by the number of descendant species as follows:

$$ED(T,i) = \sum_{e \in q(T,i,r)} \left(\lambda \frac{1}{S_e}\right) \quad (1)$$

where e is a branch of length λ in the set $s(T,i,r)$ of the tree T, connecting species i to the root r, and S_e is the number of species that descend from edge e. The phylogenetic tree used in the present analyses was generated based on the megatree R20120829 (available at https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new), which was constructed based on the phylogenetic relationships proposed by APGIII (2009). The tree branch lengths were calibrated using clade age estimates provided by Bell et al. (2010). As described above (*Woody species occurrence* section), the species pool used for the calculation of the evolutionary distinctiveness was based in the most comprehensive dataset (3,145 species).

The species index of relative rarity (IR) for each species of the Atlantic Forest complex was calculated considering the relative singularity of each species among the three different forest types. It was calculated in two steps (equations 2 and 3). First, we calculated how common each species is in the Atlantic forest by the index C, as follows:

$$C(i) = \sum_{f} \frac{n_{if}}{N_f} \frac{P_i}{F} \quad (2)$$

Where, for a given species i, n_{if} is the number of sites in the forest type f in which the species i occurs, N_f is the total number of sites in the forest type f, with f comprising the set of forest types (Dense, Mixed and Seasonal), P_i is the number of forest types in which the species i is present and F is the number of forest types. After calculating how common each species is (C), we calculated the index of relative rarity (IR) by standardizing each species C values by the maximum value found among all species and then subtracted it from 1, providing the

relative rarity of each species (*IR)*, with values ranging from 0 to 1, assigning values closer to 1 to rarer species. The IR was calculated by the equation:

$$IR(i) = 1 - \left(\frac{C_i}{C_I}\right) \quad (3)$$

Where C_i is how common a given species *i* is (equation 3), and C_I is the greater *C* value found among the species in our dataset.

Finally, with the IR and the ED values for each species, we calculated the BC for each site by the equation:

$$BC(j) = \frac{1}{3}\left[\left(\frac{1}{S_j}\sum_{i}^{S_j} IR(i)\right)_j + \left(\frac{1}{S_j}\sum_{i}^{S_j} ED(i)\right)_j + \left(\frac{S_j}{SF_j}\right)\right] \quad (4)$$

In the equation, for a given site *j*, *IR(i)* and *ED(i)* are, respectively, the *IR* and the *ED* of the species *i* occurring in site *j*, S_j is the number of species in the site *j* and SF_j is the total number of species in the forest type of site *j*. The BC of a given site thus equally weights the proportional number of species present in a site, the average rarity of these species, and their average evolutionary distinctiveness.

Deforestation rates

We used the total area of remaining forest in each municipality and the annual deforestation rate (applying for each municipality the deforestation rate found for their state; available at www.sosma.org.br, accessed in November 2015) to assess how annual deforestation rates in the Atlantic Forest region affect biodiversity. We modeled the number of species (S) per area relationship for each forest type (Dense: $S=2.718^{\{3.791 + 0.576[(\log_{2.718}\mathbf{Area}) + 0.006]\}}$; Mixed: $S=2.718^{\{3.080 + 0.577[(\log_{2.718}\mathbf{Area}) + 0.002]\}}$; Seasonal: $S=2.718^{\{3.461 + 0.577[(\log_{2.718}\mathbf{Area}) + 0.005]\}}$, and the average revenue per cropland area (US$/ha) for each municipality, based on

our empirical data. For each site, we used the modeled species richness value per area to predict the annual number of species that are lost by the deforested areas each year, as well the annual revenue that could be generated by the cropland production in these areas. Finally, we compared (student's t-test), the average proportion of revenue that could be increased by the cropland production on the deforested areas with the average proportion of the species that are lost yearly by deforestation of these areas, for each forest type.

Land use scenarios

To show how land-use allocation affects crop revenues and biodiversity, we compared biodiversity and crop revenue under three different plausible scenarios of land allocation for hypothetical farms with 10 ha in all forest types. In all scenarios, we kept 10% of the total farm area (1 ha) as hypothetical lodging area (not for production or conservation). Scenario I is the least conservative— only 10% of the farm area is allocated to conservation of natural vegetation, while 80% is allocated to croplands. Scenario II represents the current Brazilian law (NVPL) for the AF region, which requires 20% of farm land to be allocated to conservation, with the remaining 70% presumably allocated to croplands. Scenario III is the most conservative— 30% of the total farm area is allocated to conservation of native vegetation and 60% to crop production. We stress that this evaluation do not consider the spatial distribution of the forest remnants neither of the croplands within the hypothetical farms. In this way, we target evaluate the effects of allocated area size, and not configuration, over the biodiversity and cropland yield.

Different land management

Differences in crop management practices can drive variation in crop profitability per area among sites. We thus compared the revenue per area of each crop, for 28 crops, among

two categories of sites differing in the revenue per area (US$/ha). The first category included the highly profitable sites, defined as producing more than 3,000 US$/ha per year; the second category included the least profitable sites, defined as producing less than 1,000 US$/ha per year. For each crop type, we divided the average revenue per area in the highly profitable sites category by the average revenue per area in the least profitable sites category. This calculation enabled us to compare how much greater the average revenue of each crop type is within the highly profitable category compared to the least profitable category.

Improvements in cropland management can directly affect ES trade-offs. To show how improving cropland management can influence agricultural net revenue, we compared ES trade-off curves between observed revenues and potential revenues. Potential revenues were based on what would be possible if each site was as profitable as the most profitable site among four neighboring sites, taking geographic proximity into account. In the present dataset, geographically closer sites within the same biological (forest type) and social (state, region) contexts are under similar environmental and social conditions. As a consequence, we further assumed that the differences in cropland revenue among spatially proximal sites (neighboring municipalities) were driven mainly by differences in local agricultural practices (e.g. selection of crop types; managements techniques; support of cooperatives). We thus calculated potential revenue by replacing the value of each site's revenue per area (US$/ha) by the higher value (most efficient in production per area) among the target site and its four most geographically proximal sites within the same forest type. In this manner, we predicted changes in ES trade-offs for all AF sites that could theoretically result from improving management in each site thereby increasing revenue per area (US$/ha) to the same level as a site's most efficient neighbor.

All analysis described above were performed in the R software (R Core Team 2014)

and the codes used are available in the **Supporting Information S1**.

RESULTS

Biodiversity metrics and the Biological Conservation index

For all forest types, species richness (S), the index of rarity (IR) and the evolutionary distinctiveness (ED) showed similar patterns in their ES trade-off curves, with IR showing slightly lower relative values than S and ED values for the same revenue (Fig. 1). Among forest types, however, the Mixed Forest showed higher differences among the biodiversity metrics at low crop revenues (less than U$20,000; Fig.1), revealing greater loss of ED than richness or IR with increases in crop revenues. The Biological Conservation (BC) index also showed similar curves to the ED, IR and S (Fig. 2), indicating that this metric appropriately summarized the information of the individual biodiversity indices (S, IR and ED; Fig. 1).

Comparing forest types

We found no significant differences in the area, number of species and the average revenue among sites in different forest types of the Atlantic Forest (respectively: F_2= 1.015, P=0.364; F_2=2.69, P=0.071; F_2=0.032, P=0.968). However, the land use trade-off curves between cropland revenue and biodiversity indices (Fig. 3) are different for Mixed Forest. Diversity declines more steeply with increases in crop revenue for Mixed Forest indicating a more pronounced trade-off for this forest than for the other AF forest types.

The Dense Forest accumulated a greater number of species, more rare species and higher evolutionary distinctiveness with increasing area (Fig. 4) than the other forest types. Moreover, the Mixed Forest, despite harboring fewer total species, including rare species (Fig. 4 a, b), accumulates the same amount of ED with increasing area as the Seasonal Forest (Fig. 4 c).

The Dense Forest harbors the highest species' richness (Fig 5 a) and average IR per unit area (Fig 5 c). However, the Mixed Forest has the highest values of ED per species for a given land area (Fig 5 b), even though it has the lowest increase in species richness and lowest increase in rare species per total number of species per unit of increasing area. Mixed and Seasonal forests showed opposite trends in the ED/S ratio: while ED/S increases with area for Seasonal forest sites, it decreases for Mixed forest sites.

Deforestation

The linear regressions describing the species per area relation for each forest type showed high values of adjusted R-square: 0.98 for Dense, 0.99 for Mixed and 0.98 for Seasonal forests (**Supporting Information S2**). Comparison of means (by student's *t*-test), showed that deforestation affects the total number of species, and a percentage basis, more than net revenue (Table 1). On average, the municipalities in Dense Forest region loses 0.76% of its biodiversity by deforestation every year, and the conversion of these deforested areas in croplands has potential to increase the crop revenue only in 0.29% of the total. For the Mixed Forest sites, the yearly deforestation causes the loss of 0.48% of species, and the deforested area has potential for increasing the total revenue by 0.19% the total revenue. The average yearly deforested area in the Seasonal Forest region leads to the loss of 1.13% of the species but only has the potential to increase the cropland revenue by 0.23%.

Land use scenarios and different land management

The forest types did not differ in the mean revenue value within each scenario ($P > 0.05$). Furthermore, the species richness increases proportionally more with preserved area than does revenue with cropland area (Fig. 6). For all forest types, moving from the scenario I to III (Fig. 6), i.e., from the most agricultural to the most forest conservation, the mean

species richness increased by about 50% of its maximum (from ~30% to ~80%) whereas the mean revenue decreased by about 20% (from ~80% to ~60%). Also, the variance in the revenue within forest types (standard deviation in Fig. 6) reveals there are differences in the revenues and diversity among sites within forest types.

Only a few crops (cocoa, fig, rubber, coconut, tangerine, orange) showed the same or lower net revenue in the highly profitable group of sites than in the least profitable group (Fig. 7). The majority of crops were 1.5 to 3 times more profitable in the highly profitable group, and papaya and mango crops can be more than 10 times more profitable in this group of sites (Fig. 7).

If each site could produce the same revenue per area as its most efficient neighbor (defined as the most profitable site among it and the four nearest neighbors), the total revenue of croplands in the Atlantic Forest region would almost double its actual crop revenue value while maintaining the same level of biodiversity (Fig. 8). The increase in efficiency of crop production relative to habitat loss would be different for each forest type. By increasing the efficiency of crop production relative to what is possible under these simulations, the Dense Forest would reach 150% of its current maximum revenue whereas the Mixed and Seasonal Forests would reach more than 200% of their current maximum.

DISCUSSION

Our study of land use trade-offs in the Atlantic Forest biodiversity conservation hotspot reveals that 1) biodiversity loss is more sensitive to land use changes than crop revenues, and 2) enhanced management practices could allow revenues to increase without biodiversity loss. These conclusions emerge, regardless of the metric of biodiversity that is used. However, achieving management outcomes that increase efficiency by maintaining higher biodiversity and increasing provisioning services depends on 1) knowledge of forest

type, 2) the fit or comparative advantage gained from planting crops in the best places, and 3) preserving species in a balanced manner across forest types.

We presented a table (Tab. 2) that summarize the main goals, hypothesis, results and discussion present in this work.

The BC index

The proposed biodiversity conservation (BC) index incorporates species richness (S), evolutionary distinctiveness (ED) and species rarity (IR), addressing multiple conservation criteria (cf. Larkin et al. 2016), and thus serves as a more comprehensive biodiversity metric within the ecosystem services trade-offs framework than, for example, species richness alone. The metric incorporates multiple dimensions of biodiversity, which can be viewed as a surrogate for regulating, supporting and cultural ecosystem services (ES), and allows examination of trade-offs between biodiversity and crop revenues, which serve as a summary measure of provisioning ES. Using the BC we can also directly show trade-offs between biodiversity and different services measured in their own units of productivity (Fig. 2). The individual biodiversity components analyzed here (S, ED, IR) showed similar patterns of accumulation with increasing area (or loss with increasing the crop revenue, along the efficiency frontier; Fig.3). However, some differences among the forest types were only revealed by examining ED patterns.

Comparing forest types

We found some slight differences in land use trade-offs among the forest types, as expected. Diversity declines more rapidly with loss of forest area in the Mixed forest compared to the Dense or Seasonal forests (Fig. 3). As a consequence, increases in allocation of land to crop production in the Mixed forest region comes at a higher cost in terms of

biodiversity loss than in the other forest types. The forest types also differ in the accumulation of biodiversity per forest area (Fig. 4). It is not surprising that the Dense forest shows the highest accumulation of biodiversity (S, IR and ED) per area, due to its environmental heterogeneity associated with a large latitudinal and altitudinal extension (IBGE 1992, Oliveira-Filho & Fontes 2000).

The Mixed Forest accumulates the same amount of evolutionary distinctiveness per area as Seasonal Forest, even though Seasonal forest accumulates more S and IR with area (Fig. 4). The distribution of evolutionary rare species (i.e. species with high values of the evolutionary distinctiveness) within formations helps to explain these contrasting patterns. The Mixed Forest is well-known to harbor species of ancient clades (e.g. Araucariaceae, Podocarpaceae, Winteraceae; Duarte et al. 2014), a fact that drives the higher ED than S and IR values for sites in this forest type. These ancient clades are represented by a few broadly-distributed species in the Mixed forest region, which leads to the pattern of decreasing ED/S with increasing area. Even small areas of the Mixed Forest tend to contain these phylogenetically rare species. Increases in forest area thus lead to the addition of species with lower ED values, decreasing the ED/S ratio as area accumulates (Fig. 5b). On the other hand, the increasing ED/S ratio per area in the Seasonal forest reveals the ED is evenly distributed among the sites in this forest type. This similarity can arise from both equity in the species distribution through the phylogeny (i.e. similar ED values among species) or similarity in the proportions of species with high and low ED values among sites.

Deforestation and Land use scenarios

Analysis of potential deforestation rates and land use alternatives reveal that biodiversity loss occurs at a faster rate than crop revenue increases with shifts in land use from forest to croplands. We want to stress that this results refers to the size of allocated land,

as we did not consider the spatial configuration of the area within farms in the scenarios analyses (i.e. how the conservation and production areas are distributed inside each hypothetical farm), factor that could affect both crop production and biodiversity. As showed, conversion of forest to croplands likely provides only a small increase in crop production and revenue at the expense of high tree biodiversity loss (Tab. 1 and Fig. 6). Furthermore, once species are lost it generally becomes more difficult and expensive to restore the same biodiversity level in the future (Liebsch et al. 2008), and may not be possible if species become regionally or globally extinct, leading to the potential for "loss-loss" outcomes (Cavender-Bares et al. 2015a). The high cost of restoration once land is cleared is well understood; the effort to restore 390,000 ha of native forest in Brazil is expected to cost around US$500 million in the first 5 years (PLANAVEG 2014). In contrast, cropland revenue has the potential to be increased without the conversion of more land to agricultural production (Muller et al. 2012). As previously demonstrated (Strassburg et al. 2014), Brazil has enough land under agricultural production (croplands and pasturelands) to meet the future demand for provisioning services while preserving remaining land for biodiversity conservation. Thus, the expansion of croplands into current forest is thus likely unnecessary for provisioning and could result in irrecoverable biodiversity losses.

Different land management

The cropland revenue per area is different among municipalities in the Atlantic Forest region. This variation can be ascribed to differences in local environmental conditions (i.e. climate, relief and soil features), crop management (i.e. plantation and harvest technique and technology applied, irrigation, fertilization) and regional market values. Also, the same crop can have higher yields per unit area in one site than in another (Fig. 6), suggesting that there is an optimal set of crops to be produced in a given area. Thus, enhanced management

practices that match crop types to land type have the potential to increase productivity in croplands. We show that Brazilian municipalities in the AF region could theoretically increase the total annual cropland revenue by more than 150% (Fig. 8 and 9). If each municipality could produce as much as its most efficient neighbor, the same revenue could be achieved as that required by a total loss of tree biodiversity with only 20% loss of plant biodiversity. The possibility to increase the provisioning services without loss of other ES was also evidenced by examination of ES trade-offs in case studies in the Americas (Cavender-Bares et al 2015b, Ewing and Runck 2015, González-Esquivel et al. 2015, Grossman 2015). Our results support the likely possibility that crop production and revenue can be enhanced alongside increased restoration and conservation of biodiversity.

CONCLUSIONS

The BC index we developed incorporates multiple dimensions of biodiversity in a single metric, and is useful for the ecosystem services trade-offs framework applied here. It is also like to be useful for different systems around the globe. Furthermore, despite similarity in trade-off patterns among individual biodiversity components, some differences in ES trade-offs among the forest types are better revealed by specific biodiversity components. This highlights the benefits of a framework that encompass more dimensions of the biodiversity than just the number of species.

Previous studies (Strassburg et al. 2014; Alves-Pinto et al. 2017) have demonstrated that Brazil has the potential to increase its cattle ranching productivity and to convert some pasturelands to croplands to enable sustainable production by 2040. The PLANAVEG (2014) provides recommendations for how to restore Brazilian forests and where funding would come from. Here we demonstrate that the potential exists to increase productivity within existing croplands in the AF region without further conversion of forest or loss of tree

biodiversity, enabling a “win-win” scenario. In summary, conversion of Atlantic Forest to croplands is not necessary to provide for humanity; emphasis on more efficient management of existing croplands will sustain biodiversity and increase provisioning services that contribute to human well-being.

ACKNOWLEDGMENTS

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TABLES

Table 1. Student's *t*-test between expected mean species loss (as proportion of the actual total number of species) and mean revenue increased (as proportion of the yearly total revenue) in the deforested areas every year, for the three forest types of the Atlantic forest.

	Species loss % (mean ± sd)	**Increased revenue %** (mean ± sd)	***P****
Dense	0.76 ±0.7	0.29 ±0.8	0.0016
Mixed	0.48 ±0.4	0.19 ±0.3	0.0291
Seasonal	1.13 ±1	0.22 ±0.6	0.0001

*For all *P*-values > 0.05, the difference is considered to be statistically significant.

FIGURES LEGENDS

Figure 1. Trade-off curves between species richness (S, black closed circle), index of rarity (IR, red inverted triangle) and evolutionary distinctiveness (ED, blue triangle) as a proportion of maximum value, and crop revenue considering all Atlantic Forest (AF) and each forest type (Dense, Mixed and Seasonal) separately.

Figure 2. Trade-off curves between Biodiversity Conservation Index (BC) as a proportion of the Atlantic Forest maximum value and the crop revenue (in $US), considering all Atlantic Forest (AF in black) and separately for each forest type (Dense in green, Mixed in red and Seasonal in blue).

Figure 3. Trade-offs' curves between a) species richness (S), b) index of rarity (IR) and c) evolutionary distinctiveness (ED), as a proportion of the maximum for each forest type and the proportion of the maximum crop revenue. Forest types: Dense (green), Mixed (red) and Seasonal (blue).

Figure 4. Accumulation curves of a) species richness (S), b) index of rarity (IR), and c) evolutionary distinctiveness (ED), as a proportion of Atlantic Forest maximum values, by proportion of AF area considering all Atlantic Forest (AF in black) and separately for each forest type (Dense in green, Mixed in red and Seasonal in blue).

Figure 5. Additive curves of a) species richness, b) ratio of Evolutionary distinctiveness per richness, and c) ratio of Index of Rarity per species richness, with Area (in thousand hectares) for all Atlantic Forest (AF in black) and separately for each forest type (Dense in green, Mixed in red and Seasonal in blue).

Figure 6. Proportion of (a) the maximum species richness and (b) the maximum crop revenue means and standard deviation for each Atlantic forest type (Dense, Mixed and Seasonal) for the three different scenarios of harvest area size and protected area size. Scenario I: 8ha for cropland and 1ha for conservation; scenario II: 7ha for cropland and 2ha for conservation; scenario III: 6ha for cropland and 3ha for conservation.

Figure 7. Relative profit for the 28 more important crops analyzed in Atlantic Forest region.

The blue bars show how many times the profit of one specific crop is greater in highly profitable sites relative to the less profitable sites. The red line represents the 1:1 line where the net crop revenue per ha in $US is the same for highly profitable and less profitable sites. Bars ending to the left of the red line show crops that return less revenue in highly profitable sites relative to less profitable sites.

Figure 8. Trade-off curves between biological conservation index (BC) as a proportion of the Atlantic Forest maximum value and the crop revenue, for all Atlantic Forest (AF in black) and for each forest type, separately for each forest type (Dense in green, Mixed in red and Seasonal in blue). Closed circles show the observed values (Obs.) and the open circles show each site's potential crop revenue values as if it could be profitable (US$/ha) as its most efficient neighbor (EN).

FIGURES

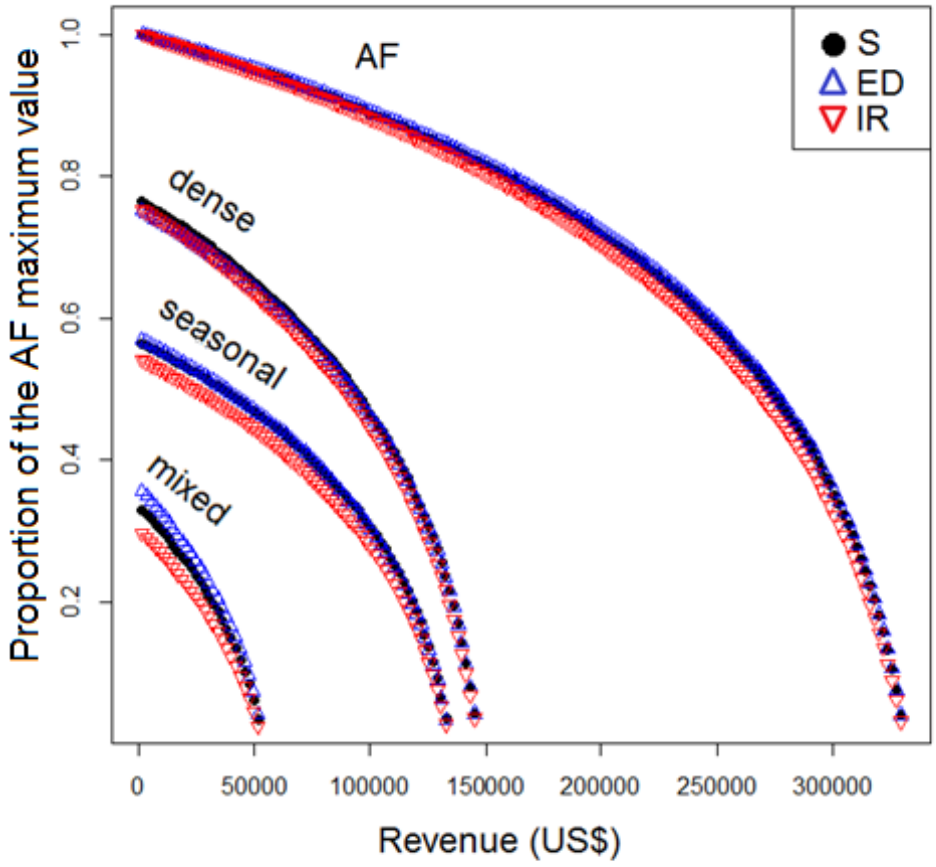

Figure 1.

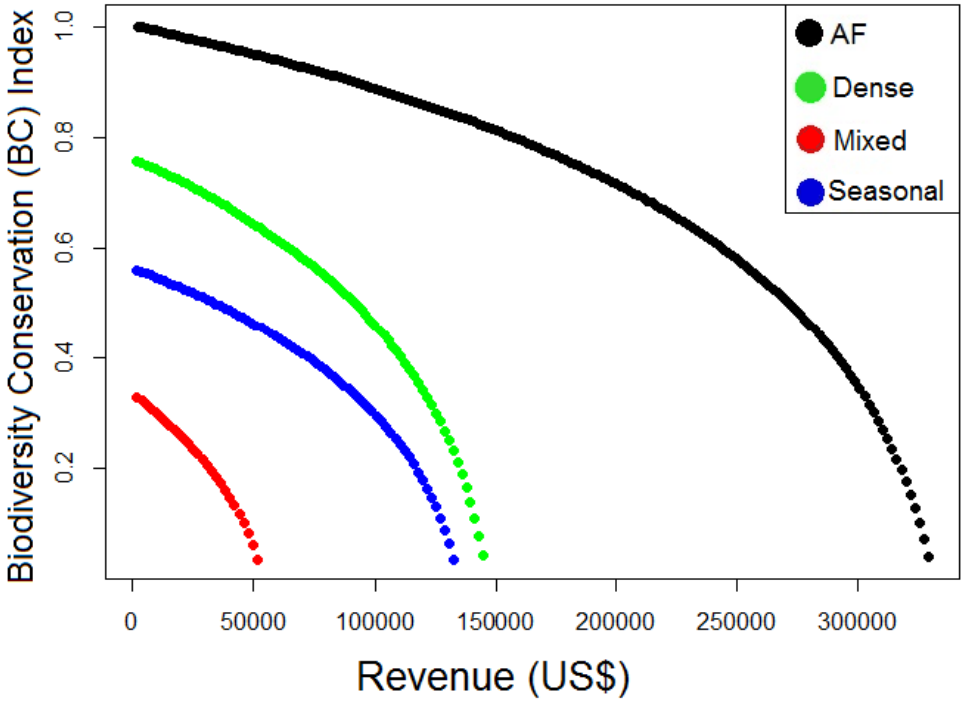
Biodiversity Conservation (BC) Index
0.2
0.4
0.6
0.8
1.0
0
50000
100000
150000
200000
250000
300000
Revenue (US$)
AF
Dense
Mixed
Seasonal

Figure 2.

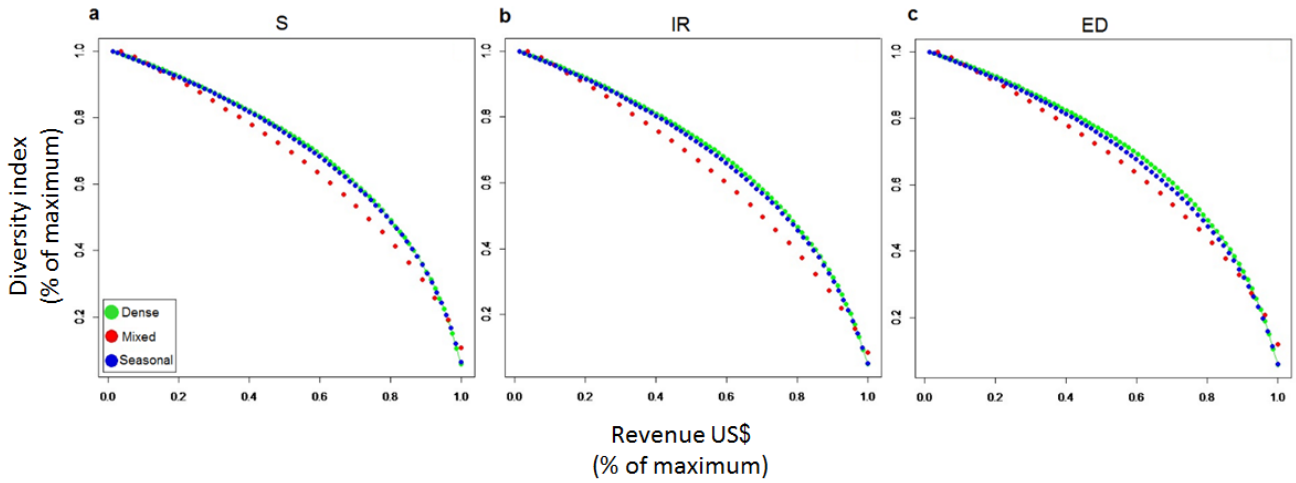
a
S
b
IR
c
ED
Diversity index
(% of maximum)
Dense
Mixed
Seasonal
0.0
0.2
0.4
0.6
0.8
1.0
Revenue US$
(% of maximum)

Figure 3.

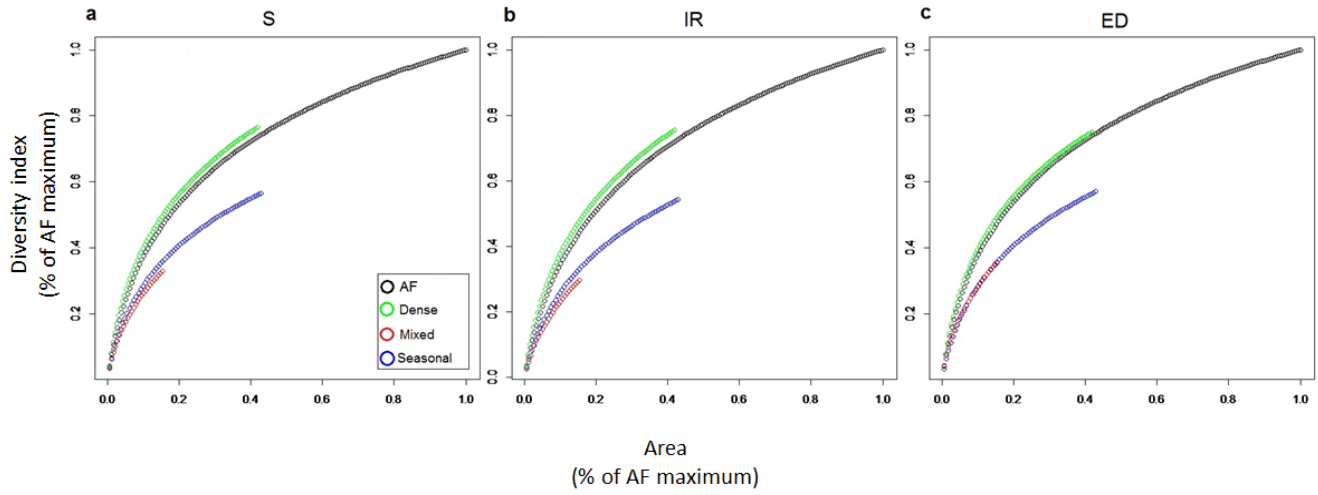
a
S
b
IR
c
ED
Diversity index
(% of AF maximum)
AF
Dense
Mixed
Seasonal
0.0
0.2
0.4
0.6
0.8
1.0
Area
(% of AF maximum)

Figure 4.

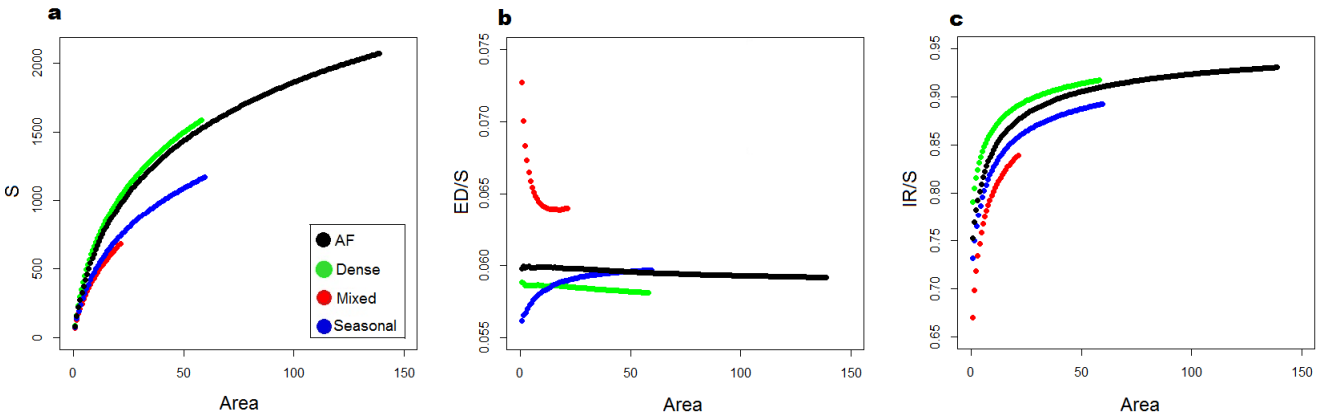

Figure 5.

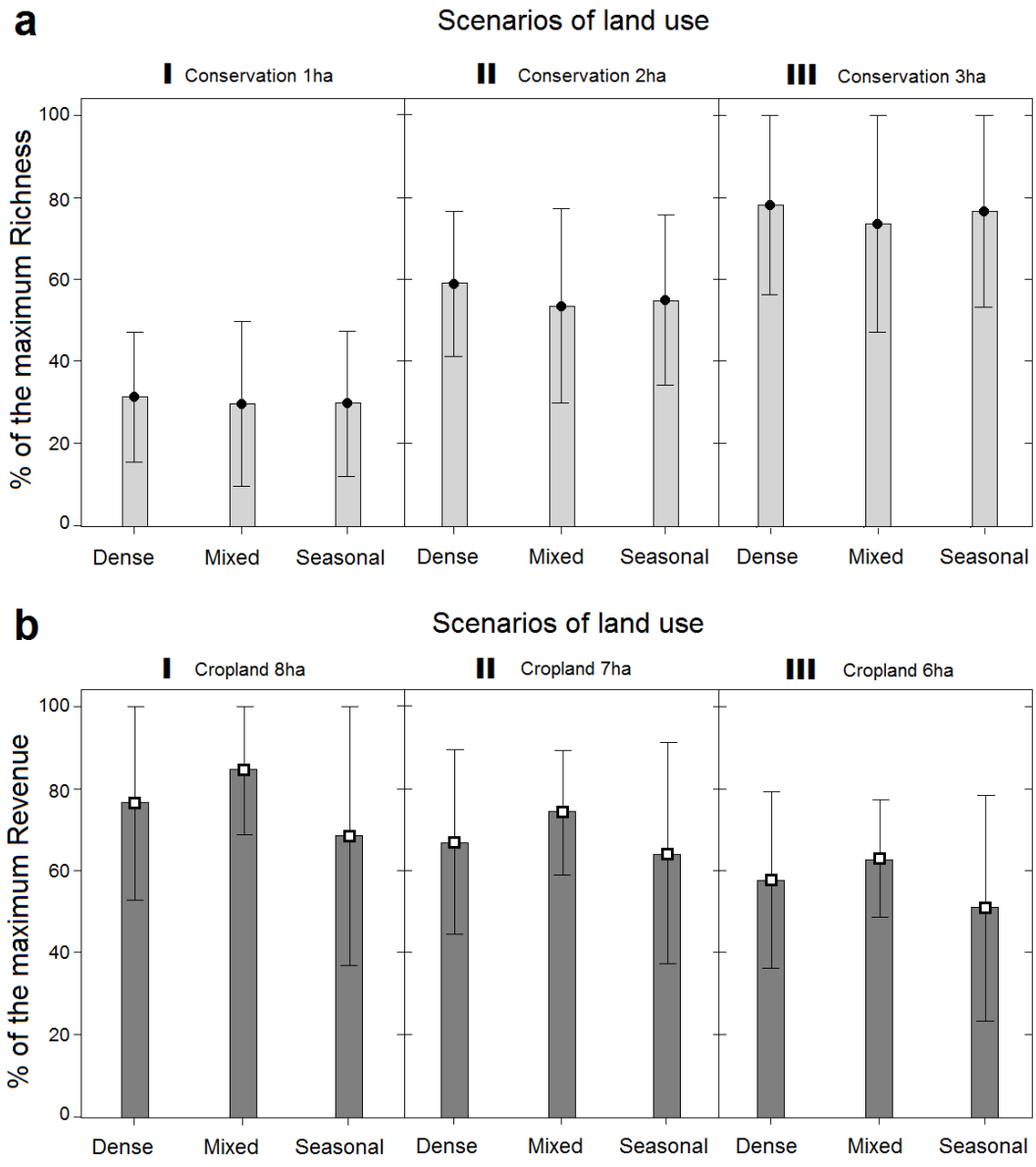
a
Scenarios of land use
I Conservation 1ha
II Conservation 2ha
III Conservation 3ha
% of the maximum Richness
100
80
60
40
20
0
Dense
Mixed
Seasonal
Dense
Mixed
Seasonal
Dense
Mixed
Seasonal
b
Scenarios of land use
I Cropland 8ha
II Cropland 7ha
III Cropland 6ha
% of the maximum Revenue
100
80
60
40
20
0
Dense
Mixed
Seasonal
Dense
Mixed
Seasonal
Dense
Mixed
Seasonal

Figure 6.

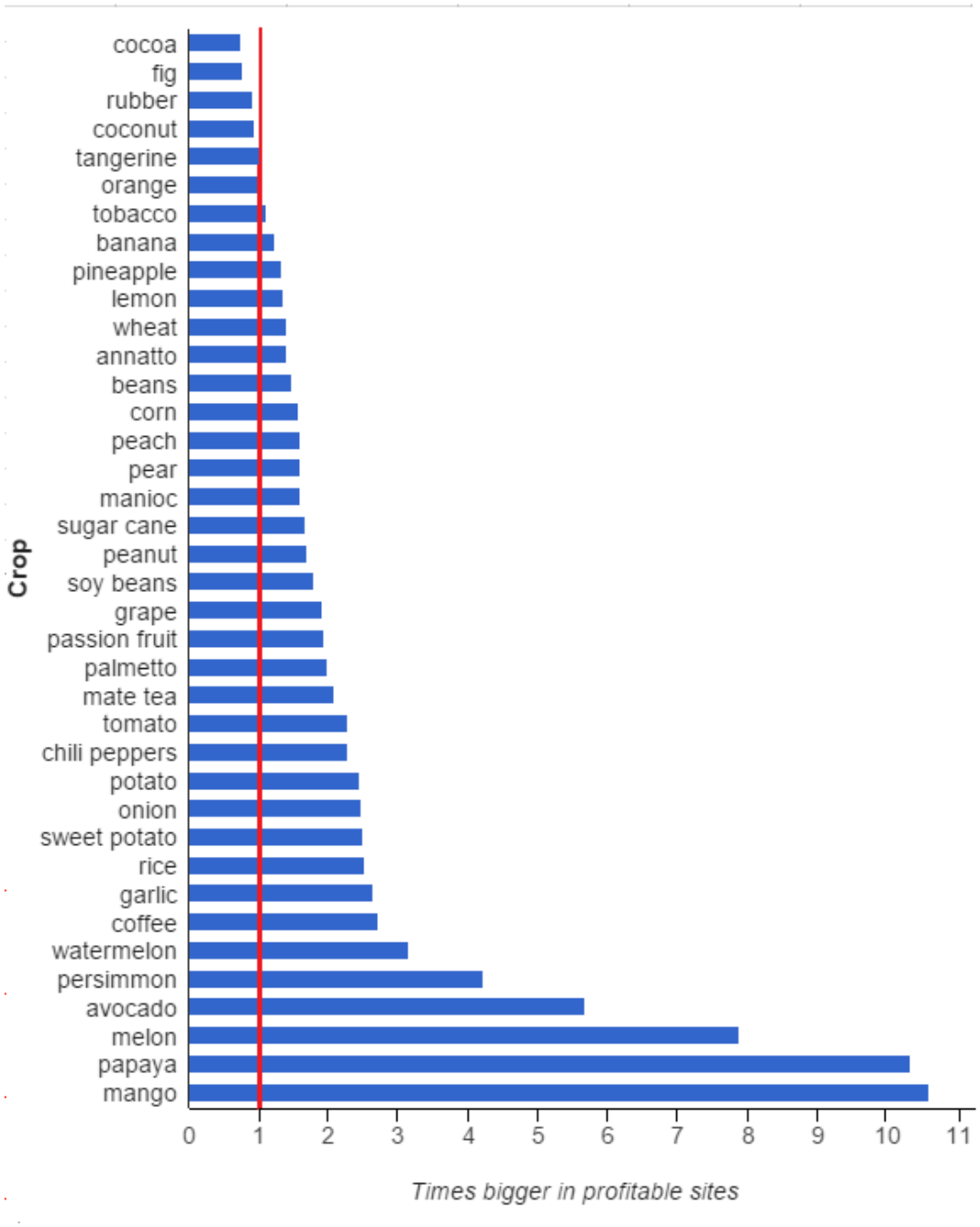
Crop
cocoa
fig
rubber
coconut
tangerine
orange
tobacco
banana
pineapple
lemon
wheat
annatto
beans
corn
peach
pear
manioc
sugar cane
peanut
soy beans
grape
passion fruit
palmetto
mate tea
tomato
chili peppers
potato
onion
sweet potato
rice
garlic
coffee
watermelon
persimmon
avocado
melon
papaya
mango
0
1
2
3
4
5
6
7
8
9
10
11
Times bigger in profitable sites

Figure 7.

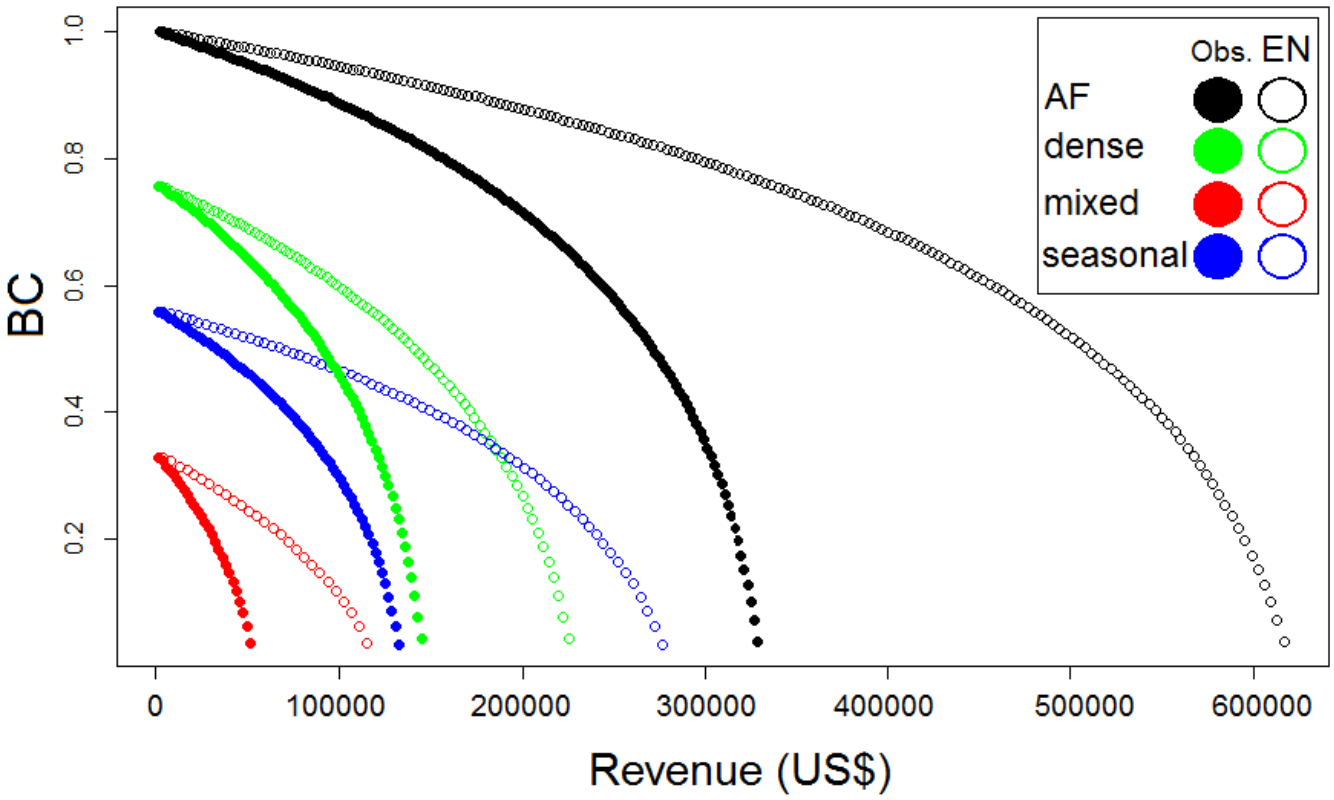
BC
1.0
0.8
0.6
0.4
0.2
0
100000
200000
300000
400000
500000
600000
Revenue (US$)
Obs. EN
AF
dense
mixed
seasonal

Figure 8.

5 CONCLUSÕES

Esse estudo traz informações valiosas para a conservação e para práticas sustentáveis do uso da terra na Floresta Atlântica. Como limitações sociais e econômicas restringem o quanto dos remanescentes florestais poderá ser conservado, é crucial investir este limitado recurso onde a biodiversidade é maximizada. A estrutura de metacomunidades observada nos remanescentes da Floresta Atlântica e de seus tipos florestais (*i.e.*, subconjunto aninhado com perda agrupada de espécies) sugere que os esforços de conservação seriam mais efetivos focando na proteção de sítios ricos em diversidade, dado que estes contêm as espécies também presentes nos sítios mais pobres. Apesar de esta estrutura ser similar entre escalas, os principais gradientes ambientais estruturando cada tipo florestal variaram. Isto enfatiza as diferenças ecológicas dessas comunidades entre escalas espaciais, e ajuda a explicar os altos índices de biodiversidade encontrados na Floresta Atlântica. Assim, além de priorizar sítios ricos em espécies, esforços de conservação devem abranger todos os tipos florestais deste bioma, garantindo a manutenção de suas características únicas.

Como visto, o homem é o responsável pela alta degradação da Floresta Atlântica, pois, historicamente, tem explorado suas riquezas de maneira imediatista e predatória. Mas as práticas de exploração econômica dessas florestas avançaram muito ao longo do desenvolvimento do Estado brasileiro. A quebra de paradigma do modelo agrícola utilizado e a aplicação de novas tecnologias trouxeram grandes avanços para a agricultura no Brasil. O momento agora é de avanço em direção à sustentabilidade, de se conciliar a produção com a conservação. O Brasil possui condições favoráveis a esse objetivo, e já mostra indícios de trilhar esse rumo. Mas somente com o uso de aplicações teóricas e tecnologias de ponta poderemos atingir a sustentabilidade e deixar para as gerações futuras as mesmas condições e oportunidades disponíveis às gerações atuais. Isto enfatiza a demanda por conhecimentos científicos que possam subsidiar melhores práticas de conservação e de intensificação da produção agrícola na Floresta Atlântica, garantindo segurança alimentar e proteção da biodiversidade nesse *hotspot*.

Evidenciamos aqui como a agricultura na Floresta Atlântica pode avançar de maneira sustentável, garantindo o aumento do bem estar humano sem a antropização dos

remanescentes florestais. Contudo, alcançar a sustentabilidade neste bioma vai depender do conhecimento dos principais determinantes ambientais da diversidade em cada tipo florestal, adequação das culturas às diferentes regiões, e da preservação de espécies de maneira balanceado entre os tipos florestais. Assim, a conversão da Floresta Atlântica em áreas agrícolas não é necessária para o homem. A ênfase no aumento de eficiência nas áreas já convertidas vai promover tanto o incremento do bem-estar humano quanto a conservação da biodiversidade.

6 ANEXOS

6.1 CAPÍTULO I

SUPPORTING INFORMATION

Appendix 1

Brief description of the sites compounding our dataset.

From the total Atlantic Forest's original cover (1,233,875 km²), Dense forest represented approximately 44% of the total area, Mixed forest 16%, and Seasonal forest 40% (Holdbrook *et al.,* 1995; Fundação SOS Mata Atlântica & INPE, 2008). From the 177 sites in our checklist, 79 sites are in the Dense forest (44%), 28 in the Mixed forest (16%) and 70 in the Seasonal forest region (40%). From the 139 ha of total sampled area, 58.13 ha are in the Dense forest (42%), 21,3 ha in the Mixed forest (15%) and 59,56 ha in the Seasonal forest (43%). Thus, the distribution of the considered sites among forest types reflects the original proportion of the Atlantic Forest that each forest type represents.

Table S1. General information (Reference source, location, area and total richness) of the Forest sites compiled in the present study.

Reference	Locality	State	Forest type	Longitude (decimal)	Latitude (decimal)	Area (ha)	Species richness (S)
Abreu *et al*., 2013	Cachoeiro de Itapemirim	ES	Seasonal	-41.283333	-20.75	2.4	53
Abreu *et al*., 2014	São Francisco de Itabapoana	RJ	Seasonal	-41.091628	-21.399842	0.4	121
Abreu *et al*., 2014	São Francisco de Itabapoana	RJ	Seasonal	-41.091628	-21.399842	0.4	65
Abreu *et al*., 2014	São Francisco de Itabapoana	RJ	Seasonal	-41.091628	-21.399842	0.4	89
Aidar *et al*., 2001	Iporanga	SP	Dense	-48.68333	-24.51667	0.1	88
Albuquerque & Rodrigues, 2000	Iperó	SP	Mixed	-47.583333	-23.416667	1.12	66
Alves Junior *et al*., 2006; Lins-e-Silva & Rodal, 2008	Recife	PE	Dense	-34.95	-8.06667	0.5	65
Andrade & Rodal, 2004	São Lourenço da Mata	PE	Dense	-35.15	-8.05	1	69
Araujo *et al*., 2004	Cachoeira do Sul	RS	Seasonal	-52.883333	-30.066667	0.58	41
Archanjo *et al*., 2012	Cachoeiro de Itapemirim	ES	Seasonal	-41.216667	-20.716667	1.25	183

Arruda & Daniel, 2007	Dourados	MS	Seasonal	-54.8	-22.216667	0.32	61
Assis *et al*., 2011	Ubatuba	SP	Dense	-44.76667	-23.33333	1	82
Assis *et al*., 2011	Ubatuba	SP	Dense	-44.85	-23.36667	1	135
Bertani *et al*., 2001	Rio Claro	SP	Seasonal	-47.716667	-22.433333	0.785	99
Bezerra de Oliveira, 2012	Moreno	PE	Dense	-35.129472	-8.115556	0.375	46
Bosa, 2011	Morro Grande	SC	Dense	-49.75	-28.73333	0.5	95
Brack, 2002	Riozinho	RS	Dense	-50.366667	-29.6	1	55
Brack, 2002	Maquiné	RS	Dense	-50.15	-29.7	1	107
Brito & Carvalho, 2014	Juiz de Fora	MG	Seasonal	-43.366667	-21.733333	1	79
Budke *et al*., 2004	Santa Maria	RS	Seasonal	-53.783333	-29.683333	1	56
Budke *et al*., 2005	Santa Maria	RS	Seasonal	-53.783333	-29.683333	1	55
Caglioni, 2013	Blumenau	SC	Dense	-49.06667	-27.03333	0.33	108
Camargos *et al*., 2008	Dionísio	MG	Seasonal	-42.466667	-19.8	1	206
Campos *et al*., 2000	Glória de Dourados	MS	Seasonal	-53.3	-22.716667	0.54	63
Campos *et al*., 2011	Ubatuba	SP	Dense	-44.81667	-23.33333	1	134
Cardoso-Leite *et al*., 2004	Rio Claro	SP	Seasonal	-47.666667	-22.583333	0.45	32
Cardoso-Leite *et al*., 2013	Barra do Turvo	SP	Dense	-48.36667	-24.55	0.8	124
Carmo & Assis, 2012	Tibagi	PR	Mixed	-50.256944	-24.652778	0.5	96
Carvalho *et al*., 2005	Bocaina de Minas	MG	Mixed	-44.566667	-22.216667	1.04	208
Carvalho *et al*., 2005	Bom Sucesso	MG	Seasonal	-44.883333	-21.15	1.125	86
Carvalho *et al*., 2005	Três Marias	MG	Seasonal	-45.166667	-18.083333	1.125	221
Carvalho *et al*., 2007	Rio Bonito	RJ	Dense	-42.61667	-22.7	0.4	143
Carvalho *et al*., 2009	Araucária	PR	Mixed	-49.33333	-25.583333	0.2	52
Carvalho, 2011	Porto Seguro	BA	Dense	-39.08333	-16.26667	1	101
Cesar & Monteiro, 1995	Ubatuba	SP	Dense	-44.84006	-23.38173	0.52	65
Christo *et al*., 2009	Silva Jardim	RJ	Dense	-42.33333	-22.51667	0.5	102
Colonetti, 2008	Siderópolis	SC	Dense	-49.55	-28.6	1	105
Cordeiro & Rodrigues, 2007	Guarapuava	PR	Mixed	-51.466667	-25.35	0.32	33
Costa Filho *et al*., 2006	Diamante do Norte	PR	Seasonal	-52.91667	-22.68333	1.5	92
Costa Jr *et al*., 2008	Catende	PE	Dense	-35.67461	-8.6305	1	78

Cruz *et al*., 2013	Macaé	RJ	Dense	-42.463889	-22.263889	0.6	112
Cunha *et al*., 2013	Mão Dágua	PB	Seasonal	-36.75333	7.07	1.8	52
Curcio *et al*., 2007	Bom Jardim da Serra (Rio do Rastro)	SC	Mixed	-51.1	-26.2	0.12	33
Curcio *et al*., 2007	Bom Jardim da Serra (Rio do Rastro)	SC	Mixed	-49.416667	-25.583333	0.12	68
da Silva *et al*., 2013	Alfredo Wagner	SC	Mixed	-49.333611	-27.700278	0.4	87
Dan *et al*., 2010	São José de Uba	RJ	Seasonal	-41.933333	-21.35	0.8	24
De Marchi & Jarenkow, 2008	Cristal	RS	Seasonal	-51.93333	-31.01667	1	29
de Paula *et al*., 2004	Viçosa	MG	Seasonal	-42.116667	-20.75	1	91
Dias *et al*., 1998	Tibagi	PR	Mixed	-50.416667	-24.516667	1	107
Dorneles & Waechter, 2004	Mostardas (Lagoa peixe)	RS	Dense	-50.834	-31.16667	0.2	25
Durigan *et al*., 2000	Gália	SP	Seasonal	-49.7	-22.4	0.6	61
Durigan, 1994	Marilha	SP	Seasonal	-49.916667	-22.016667	0.3	63
Durigan, 1994	Taruma	SP	Seasonal	-50.516667	-22.7	0.3	65
Durigan, 1994	Taruma	SP	Seasonal	-50.666667	-22.816667	0.3	60
Fagundes *et al*., 2007	Passos	MG	Dense	-46.45	-20.666667	0.52	65
Fagundes *et al*., 2007	Alinópolis	MG	Seasonal	-46.366667	-20.683333	0.48	43
Feitosa, 2004	Recife	PE	Dense	-34.95	-8.1	1	40
Ferreira Jr., 2005	Viçosa	MG	Seasonal	-42.75	-20.75	1	121
Floss, 2011	Ponte Serrada	SC	Mixed	-51.96667	-26.81667	1.56	57
Floss, 2011	Saudades	SC	Seasonal	-53.03333	-26.86667	1.56	84
Floss, 2011	Guatambu	SC	Seasonal	-52.76667	-27.1	1.56	74
Fonseca & Carvalho, 2012	Juiz de Fora	MG	Seasonal	-43.366667	-21.733333	1	66
Gandra *et al*., 2011	Itaguaí	RJ	Dense	-43.81667	-22.8	0.5	75
Giehl & Jarenkow, 2008	Barra do Guarita (Turvo)	RS	Seasonal	-53.883333	-27.15	1	80
Giehl *et al*., 2007	Santa Maria	RS	Seasonal	-53.9	-29.633333	1	56
Giongo & Waechter, 2007	Encruzilhada do Sul	RS	Mixed	-52.7	-30.5	0.3	41
Gomes *et al*., 2004	Pindamonhangaba	SP	Dense	-45.53333	-22.8	0.25	68
Gomes *et al*., 2011	Ubatuba	SP	Dense	-45.06667	-23.36667	1	146
Gomes *et al*., 2011	Faxinalzinho	SP	Dense	-45.08333	-23.36667	1	184

Gris, 2012	Santa Terezinha do Itaipu/São Miguel do Iguacu	PR	Seasonal	-54.28333	-25.51667	0.36	54
Gris, 2012	Santa Terezinha do Itaipu/ São Miguel do Iguacu	PR	Seasonal	-54.33333	-25.51667	0.36	61
Gris, 2012	Santa Terezinha do Itaipu/ São Miguel do Iguacu	PR	Seasonal	-54.35	-25.48333	0.36	65
Gris, 2012	Santa Terezinha do Itaipu/ São Miguel do Iguacu	PR	Seasonal	-54.35	-25.46667	0.36	49
Gris, 2012	Santa Terezinha do Itaipu/ São Miguel do Iguacu	PR	Seasonal	-54.35	-25.45	0.36	41
Guidini *et al*., 2014	Lages	SC	Mixed	-50.325	-27.816111	1	70
Guidini *et al*., 2014	Lages	SC	Mixed	-50.325	-27.816111	1	66
Guilherme *et al*., 2004	Sete Barras	SP	Dense	-48.06667	-24.23333	0.99	242
Holanda, 2008; Oliveira, 2006	Nazaré da Mata	PE	Dense	-35.2	-7.73333	1.26	55
Ivanauskas & Rodrigues, 2000	Piracicaba	SP	Seasonal	-47.65	-22.65	0.43	76
Ivanauskas *et al*., 1999	Itatinga	SP	Seasonal	-48.55	-23.28333	0.42	83
Ivanauskas, 1997	Pariquera-Açu	SP	Dense	-47.88333	-24.6	1.21	158
Iza, 2002	Ilhota	SC	Dense	-48.95	-26.78333	1	135
Jarenkow & Baptista, 1987	Muitos Capões	RS	Seasonal	-51.166667	-28.216667	0.48	50
Jarenkow & Waechter, 2001	Vale do Sol	RS	Seasonal	-52.66667	-29.56667	1	55
Jarenkow, 1994	Morrinhos do Sul	RS	Dense	-49.966667	-29.35	1	60
Jurinitz & Jarenkow, 2003	Camaquã	RS	Dense	-51.88333	-30.68333	1	69
Klauberg *et al*., 2010	Lages	SC	Mixed	-50.35	-27.78333	0.64	45
Kurtz & Araújo, 2000	C. do Macacu	RJ	Dense	-42.88333	-22.46667	0.44	114
Kurtz *et al*., 2009	Cabo Frio	RJ	Seasonal	-41.95	-22.8	0.5	83
Leite & Rodrigues, 2008	São Roque	SP	Seasonal	-47.1	-23.516667	0.945	112
Leyser et al., 2009	Faxinalzinho	RS	Mixed	-52.666667	-27.333333	1	71
Lima *et al*., 2010	Corumbá	MS	Seasonal	-57.666667	-19.016667	0.22	50
Lindenmaier & Budke, 2006	Cachoeira do Sul	RS	Seasonal	-52.8	-30	1	48
Longhi *et al*., 1999	Santa Maria	RS	Seasonal	-53.783333	-29.683333	0.36	54
Longhi *et al*., 2008	Montenegro	RS	Seasonal	-51.416667	-29.816667	1.8	73
Lopes, 2007	São Vicente Férrer	PE	Dense	-35.46667	-7.61667	1	87

Lopes, 2007	Aliança	PE	Seasonal	-35.25	-7.66667	1	54
Loures *et al*., 2007	Santa Rita de Caldas	MG	Mixed	-46.35	-22.083333	1	103
Machado *et al*., 2004	Lavras	MG	Seasonal	-44.966667	-21.216667	1.16	142
Magnago *et al*., 2011	Serra	ES	Dense	-40.21667	-20.15	0.6	66
Marchi & Jarenkow, 2008	Cristal	RS	Seasonal	-51.933333	-31.016667	1	23
Martini *et al*., 2007	Uruçuca	BA	Dense	-39.1	-14.48333	0.1	100
Martini *et al*., 2007	Uruçuca	BA	Dense	-39.05	-14.35	0.1	101
Martini *et al*., 2007	Uruçuca	BA	Dense	-39.06667	-14.38333	0.1	103
Martins, 2005	Siderópolis	SC	Dense	-49.4	-28.57	1	108
Martins, 2010	Araranguá	SC	Dense	-49.51667	-29.03333	1	26
Martins, 2010	Timbé do Sul	SC	Dense	-49.83333	-28.73333	1	142
Medeiros & Aidar, 2011	Natividade da Serra	SP	Dense	-45.116667	23.583333	0.6	69
Melo *et al*., 2000	Iguape (E.E. Jureia)	SP	Dense	-47.25	-24.5	1	157
Moraes & Mondin, 2001	Palmares	RS	Dense	-50.3	-30.35	0.1	31
Nascimento *et al*., 1999	Piracicaba	SP	Seasonal	-47.816667	-22.783333	0.5805	45
Nascimento, 2001	Brejo da Madre de Deus	PE	Dense	-36.38333	-8.18333	1	47
Negrelle, 2006	Itapoá	SC	Dense	-48.63333	-26.06667	1	119
Negrini *et al*., 2012	Lages	SC	Mixed	-50.325	-27.816111	1	86
Negrini *et al*., 2014	Lages	SC	Mixed	-50.325	-27.816111	1	71
Nunes *et al*., 2003	Lavras	MG	Seasonal	-44.95	-21.216667	5.04	41
Nunes, 2001	Dom Pedro de alcântara	RS	Dense	-49.08333	-29.383333	0.35	77
Oliveira & Rotta, 1982	Colombo	PR	Mixed	-49.233333	-25.33333	0.72	54
Oliveira *et al*., 2001	Peruibe	SP	Dense	-47	-24.28333	0.2	44
Oliveira *et al*., 2012	Salgado	SE	Seasonal	-37.46667	-10.66667	0.79	71
Oliveira, 2006	Aliança	PE	Dense	-35.15	-7.46667	0.26	39
Oliveira, 2006	Timbaúba	PE	Dense	-35.36667	-7.43333	0.26	37
Oliveira, 2008	Morro da Fumaça	SC	Dense	-49.35	-28.63333	0.125	42
Oliveira-Lima, 2012	Guarapuava	PR	Mixed	-51.398611	-25.325	0.66	48
Padgurschi *et al*., 2011	Sao Luiz do Paraitinga	SP	Dense	-45.05	-23.28333	1	147
Padgurschi *et al*., 2011	Sao Luiz do Paraitinga	SP	Dense	-45.18333	-23.4	1	121

Pompeu *et al*., 2014	Itamonte	MG	Dense	-44.815278	-22.3775	0.6	88
Quiqui *et al*., 2007	Diamante do Norte	PR	Seasonal	-54.816667	-22.566667	0.435	59
Ribas *et al*., 2003	Viçosa	MG	Seasonal	-42.8	-20.8	0.2	53
Ribeiro *et al*., 2013	Bananal	SP	Mixed	-44.366111	-22.806667	0.86	138
Ríos et al., 2008	Paraíso (Misiones)	SC	Mixed	-53.933333	-26.5	1.64	25
Rocha, 2007	Igarassu	PE	Dense	-34.98333	-7.81667	1	84
Rochelle *et al*., 2011	Ubatuba	SP	Dense	-45.08333	-23.35	1	177
Rondon Neto *et al*., 2002	Caxias do Sul	RS	Mixed	-50.916667	29	0.8	35
Rosa *et al*., 2008	Tupanciretã	RS	Seasonal	-53.833333	-29.066667	0.2	24
Rotta *et al*., 1997	Paranaguá (P.E. do Palmito)	PR	Dense	-48.53333	-25.58333	0.28	87
Ruschel *et al*., 2007	Barra do Guarita (Turvo)	RS	Seasonal	-53.85	-27.183333	0.4	51
Sambuichi, 2002	Ilhéus	BA	Dense	-39.25	-14.6	2.6	30
Santos, 2003	Siderópolis	SC	Dense	-49.4	-28.56667	0.5	83
Santos, 2003	Siderópolis	SC	Dense	-49.38333	-28.56667	0.5	77
Santos, 2005	Viçosa	MG	Seasonal	-42.91667	-20.75	0.5	123
Scherer *et al*., 2005	Viamao	RS	Dense	-51	-30.36667	1.02	28
Schorn & Galvão, 2009	Blumenau	SC	Dense	-49.01667	-27.01667	1.2	79
Schorn, 2005	Blumenau	SC	Dense	-49.06667	-27.05	0.4	80
Silva & Scariot, 2003	São Domingos	GO	Seasonal	-46.683333	-13.816667	1	28
Silva & Scariot, 2004	São Domingos	GO	Seasonal	-46.733333	-13.683333	1	40
Silva & Soares, 2002	São Carlos	SP	Seasonal	-47.8	-21.91667	1	64
Silva *et al*., 2003	Ibituruna	MG	Seasonal	-44.83333	-21.15	1.04	110
Silva Jr, 2004	Cabo de Santo Agostinho	PE	Dense	-35.03333	-8.16667	1	93
Silva, 1994	Morretes	PR	Dense	-48.9	-25.5	0.13	73
Silva, 2006	Criciúma	SC	Dense	-49.41667	-28.8	1	132
Silva, 2009	Sirinhaém	PE	Dense	-35.16667	-8.56667	1.5	86
Simonelli *et al*., 2008	Linhares	ES	Dense	-39.89	-19.08333	1	60
Siqueira *et al*., 2009	Araguari	MG	Seasonal	-48.1	-18.783333	1.2	232
Siqueira *et al*., 2009	Araguari	MG	Seasonal	-48.116667	-18.8	1.2	35
Soares, 2005	Araponga	MG	Seasonal	-42.49611	-20.68972	0.34	125

Sobrinho et al., 2008	Nova Iguaçu	RJ	Dense	-43.4	-22.58333	0.2	44
Sonego *et al*., 2007	São Francisco de Paula	RS	Mixed	-50.38333	-29.38333	0.29	40
Souza *et al*., 2012	Campos do Jordão	SP	Mixed	-45.464444	-22.691667	1	52
Souza Jr, 2006	Recife	PE	Dense	-34.91667	-8.06667	1	72
Tanaka, 2009	Riberão Preto	SP	Seasonal	-47.833333	-21.216667	1.08	121
Tavares, 1998	Caruaru	PE	Dense	-36	-8.3	1	60
Teixeira, 2009	Tamandaré	PE	Dense	-35.18333	-8.73333	1.05	77
Teo *et al*., 2012	Lebon Régis	SC	Mixed	-50.68333	-26.91667	1	51
Teo *et al*., 2014	Lebon Régis	SC	Mixed	-50.679553	-26.893981	1	35
Thomas *et al*., 2008	Uruçuca	BA	Dense	-39.01667	-14.411	1	207
Unesc, 2009	Criciúma	SC	Dense	-49.35	-28.68333	0.285	84
Van den Berg & Oliveira-Filho, 2000	Itutinga	MG	Seasonal	-44.6	-21.35	0.84	154
Viani *et al*., 2011	Quedas do Iguaçu	PR	Seasonal	-52.81667	-25.46667	0.5	65
Viani *et al*., 2011	Quedas do Iguaçu	PR	Seasonal	-52.96667	-25.55	0.61	73
Viani *et al*., 2011	Quedas do Iguaçu	PR	Seasonal	-52.88333	-25.48333	0.52	59
Vitória, 2009	Itambé	PE	Dense	-35.16667	-7.5	0.5	30
Vitória, 2009	Itambé	PE	Dense	-35.18333	-7.41667	0.5	34
Warley *et al*., 2007	Piedade do Rio Grande	MG	Dense	-44.1	-21.483333	1.2	112
Xavier, 2009	Dona Inês	PB	Dense	-35.6	-6.61667	0.35	44
Xavier, 2009	Dona Inês	PB	Dense	-35.61667	-6.63333	0.37	38
Zacarias, 2008	Guaraqueçaba	PR	Dense	-48.45	-25.15	0.16	77

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6.2 SUPPORTING INFORMATION

Appendix 2

Effects of the number of sites on the elements of metacommunity structure of the Atlantic Forest.

Table 1. Elements of metacommunity structure analysis based in 28 sites sorted from the total number of sites for the Dense and Seasonal forest types. Mean and standard deviation based in 100 simulations.

	Coherence		Turnover		Boundary clumping	
Forest type (total number of sites)	Observed value for all sites	Simulation mean (sd)	Observed value for all sites	Simulation mean (sd)	Observed value for all sites	Simulation mean (sd)
Dense (78)	2.48	4.57 (0.55)	-2.97	-1.04 (0.19)	7.94	1.62 (0.26)
Seasonal (70)	2.01	3.24 (1.10)	-3.1	-1.06 (0.19)	5.7	1.71 (0.20)

CAPÍTULO III

Supporting Information S1: *R Codes*

Preparing community presence data for the analysis

#From a species (rows) by sites (columns) incidence matrix with the first row describing #forest type and the second row describing the site total area.

```
prep = function(COM){
COM=as.matrix(COM)
prepa=matrix(0,length(COM[,1]), (length(COM[1,]))-1)
prepa[1,]=COM[1,-1]
for (i in 2:length(COM[,1])){
for (j in 2: length(COM[1,])){
prepa[i,(j-1)]=(if((as.numeric(COM[i,j]))==1){COM[i,1]} else{0})}
}
return(prepa)
```

```
}
```

Calculating the IR (rarity) for each species

```
IR = function(tfcom){

Nden=sum(tfcom[1,]=="den") #sum of sites in the formation

Nmix=sum(tfcom[1,]=="mix")

Nsea=sum(tfcom[1,]=="sea")

# IR calculation

IRres=matrix(0,nrow=length(tfcom[,1])-1,ncol=5) # creating the result matrix

for (i in 2:length(tfcom[,1])){

# first term of IR equation

IRres[i-1,2] =
((sum(as.numeric(as.matrix(tfcom[i,tfcom[1,]=="den"])))/Nden)+((sum(as.numeric(as.matrix(tfcom[
i,tfcom[1,]=="mix"])))/Nmix)+((sum(as.numeric(as.matrix(tfcom[i,tfcom[1,]=="sea"])))/Nsea)

# second term (P) of IR equation

IRres[i-1,3] =
((if(((sum(as.numeric(as.matrix(tfcom[i,tfcom[1,]=="den"])))/Nden)>0){1}else{0})+(if(((sum(as.nu
meric(as.matrix(tfcom[i,tfcom[1,]=="mix"])))/Nmix)>0){1}else{0})+(if(((sum(as.numeric(as.matrix
(tfcom[i,tfcom[1,]=="sea"])))/Nsea)>0){1}else{0}))

IRres[i-1,4] = (as.numeric(IRres[i-1,2]))*(as.numeric(IRres[i-1,3]))#
*((sum(as.numeric(as.matrix(tfcom[i,-1])))/length(tfcom[1,-1])) #IR

}

for (j in 1:length(IRres[,1])){

# IR normalized by its maximum, without zero (0=0.001)

IRres[j,5] = ((((as.numeric(IRres[j,4])/as.numeric(max(IRres[,4])))-1)*-1)+0.001)

}

IRres[,1] = as.matrix(tfcom[-1,1])  #Adding the species names

return(IRres)

}
```

Preparing the LIST (IR + ED), for BC calculation

```
AF.list=matrix(0, nrow=(length(ED[,1])),3)

pos=as.matrix(na.omit(match(ED[,1],IR.AFall[,1])))

for (j in 1:(length(ED[,1]))){

AF.list[j,3]<-(IR.AFall[(pos[j,1]),5])
```

```
}
AF.list[,1]<-as.matrix(ED[,1])
AF.list[,2]<-ED[,2]
```

Calculating the BC Index for sites (COM and LIST need to be prepared first, as presented above)

```
index.site=function (COM,LIST){
res=matrix(0,5,length(COM[1,]))
for (i in 1:length(COM[1,])){
res[1,i]=length(as.matrix(na.omit(match(unique(c(COM[,i])),LIST)))) #S
index=matrix(0, nrow=(length(as.matrix(na.omit(match(unique(c(COM[,i])),LIST))))),2)
for (j in 1:(length(as.matrix(na.omit(match(unique(c(COM[,i])),LIST)))))){
index[j,1]<-LIST[(as.matrix(na.omit(match(unique(c(COM[,i])),LIST)))[j,1]),2]
index[j,2]<-LIST[(as.matrix(na.omit(match(unique(c(COM[,i])),LIST)))[j,1]),3]
}
res[2,i]=sum(as.numeric(index[,1]))
res[3,i]=mean(as.numeric(index[,1]))
res[4,i]=sum(as.numeric(index[,2]))
res[5,i]=mean(as.numeric(index[,2]))
}
results<-data.frame(res)
rownames(results)=c("S","ED.sum", "ED.mean","IR.sum", "IR.mean")
return(results)
}
```

Building the Trade-offs additive curves, with mean and sd (COM and LIST #need to be prepared first, as presented above)

```
AddCurv = function(COM, LIST, RND){
res=array(0, dim=c(length(COM[1,]),7,RND))
rest=matrix(0,length(COM[1,]),13)
for (k in 1:RND){
```

```
COM=COM[,sample(ncol(COM))] # ordering columns at random
for (i in 1:(length(COM[1,]))){
res[i,1,k]=i
res[i,2,k]=sum(as.numeric(COM[1,1:i])) # area
pos=as.matrix(na.omit(match(unique(c(COM[-1, 1:i])),LIST)))
res[i,3,k]<- length(pos)
index=matrix(0, nrow=(length(pos[,1])),2)
for (j in 1:(length(pos[,1]))){
index[j,1]<-LIST[(pos[j,1]),2]
index[j,2]<-LIST[(pos[j,1]),3]
}
res[i,4,k]<-sum(as.numeric(index[,1]))
res[i,5,k]<-sum(as.numeric(index[,2]))
res[i,6,k]<-mean(as.numeric(index[,1]))
res[i,7,k]<-mean(as.numeric(index[,2]))
}
}
for (l in 1:RND){
for (m in 1:length(COM[1,])){
rest[m,1]=m
rest[m,2]= mean(res[m,2,(1:l)])
rest[m,3]= sd(res[m,2,(1:l)])
rest[m,4]= mean(res[m,3,(1:l)])
rest[m,5]= sd(res[m,3,(1:l)])
rest[m,6]= mean(res[m,4,(1:l)])
rest[m,7]= sd(res[m,4,(1:l)])
rest[m,8]= mean(res[m,5,(1:l)])
rest[m,9]= sd(res[m,5,(1:l)])
rest[m,10]= mean(res[m,6,(1:l)])
rest[m,11]= sd(res[m,6,(1:l)])
```

```
rest[m,12]= mean(res[m,7,(1:l)])
rest[m,13]= sd(res[m,7,(1:l)])
}
}
results<-data.frame(rest)
colnames(results)=c("sites.N", "Area.mean", "Area.sd","S.mean", "S.sd","ED.mean",
"ED.sd","IR.mean", "IR.sd","ave.ED.mean", "ave.ED.sd","ave.IR.mean", "ave.IR.sd")
return(results)
}
```

Plotting all 3 biodiversity index (S, IR, ED; colors) by formation (symbols)

```
plot(rev(add.yield.AF[,4]),sci.AF[,3],xlab="Yield $", ylab="Index",pch=0,col="black")
points(rev(add.yield.den[,4]),sci.den[,3],col="black",pch=1)
points(rev(add.yield.sea[,4]),sci.sea[,3],col="black",pch=2)
points(rev(add.yield.mix[,4]),sci.mix[,3],col="black",pch=6)
points(rev(add.yield.AF[,4]),sci.AF[,4],pch=0,col="blue")
points(rev(add.yield.den[,4]),sci.den[,4],col="blue",pch=1)
points(rev(add.yield.sea[,4]),sci.sea[,4],col="blue",pch=2)
points(rev(add.yield.mix[,4]),sci.mix[,4],col="blue",pch=6)
points(rev(add.yield.AF[,4]),sci.AF[,5],col="red",pch=0)
points(rev(add.yield.den[,4]),sci.den[,5],col="red",pch=1)
points(rev(add.yield.sea[,4]),sci.sea[,5],col="red",pch=2)
points(rev(add.yield.mix[,4]),sci.mix[,5],col="red",pch=6)
```

Plotting BC for all forest types by area

```
plot(sci.AF[,2],sci.AF[,6],xlab="Area", ylab="SCI")
points(sci.sea[,2],sci.sea[,6],col="blue")
points(sci.mix[,2],sci.mix[,6],col="red")
points(sci.den[,2],sci.den[,6],col="green")
```

Plotting trade-off curves between BC and revenue for all forest types

```
plot(rev(add.yield.AF[,4]),sci.AF[,6],xlab="Revenue (US$)", ylab="SCI",pch=16)
points(rev(add.yield.den[,4]),sci.den[,6],col="green",pch=16)
points(rev(add.yield.sea[,4]),sci.sea[,6],col="blue",pch=16)
```

```
points(rev(add.yield.mix[,4]),sci.mix[,6],col="red",pch=16)
```

Supporting Information 2: *Modeling the Atlantic Forest and its forest types species area relationships by regressions.*

Dense forest (Adjusted R^2: 0.9778):

$$\log(S) = 3.7910 + 0.5759 \times [\log(Area_{Km2})] \pm 0.0063$$

Mixed forest (Adjusted R^2: 0.9933):

$$\log(S) = 3.0803 + 0.6519 \times [\log(Area_{Km2})] \pm 0.0020$$

Seasonal forest (Adjusted R^2: 0.9821):

$$\log(S) = 3.4611 + 0.5767 \times [\log(Area_{Km2})] \pm 0.0049$$

Atlantic forest (Adjusted R^2: 0.9677):

$$\log(S) = 4.0508 + 0.5085 \times [\log(Area_{Km2})] \pm 0.0079$$